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Comparison of Inlet and Outlet Spawning Runs of Rainbow Trout in Loon Lake, British Columbia[1]

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ABSTRACT

Rainbow trout (*Salmo gairdneri*) entering and leaving inlet and outlet spawning streams were trapped and marked during three years. Spawners entered the outlet stream at approximately the same time each year despite considerable differences in time of lake ice breakup. Spawners entered the inlet stream 3 to 5 weeks later than outlet spawners and at water temperatures several degrees higher. The inlet spawning run was later in years when disappearance of lake ice was delayed. Comparative statistics are presented on size, sex ratio, survival and diel movement of spawners in both streams. Effects of several types of marking were compared; removal of adipose fins produced much lower mortality than tagging with Petersen discs. In the outlet stream an inverse correlation existed between number of spawners and survival, condition, and length of stay of spawners in the stream. Factors which may be responsible for differences in timing of spawning migrations are discussed.

INTRODUCTION

In the course of a study on the homing of rainbow trout spawners at Loon Lake (Lindsey *et al.*, 1959), and on the stream current responses of young fish, considerable information also was gathered on comparative statistics of spawning runs to the inlet and outlet streams. Although inlet spawning runs of rainbow trout have been studied extensively (Mottley, 1933; Rayner, 1942), little has been published concerning spawning runs to outlet streams. The present paper summarizes information on timing, survival, size composition, and other features of the life history during reproduction. The various factors which may control movement of trout during their spawning migration into inlet and outlet streams cannot be examined in detail with data available, but some speculation on their possible roles is presented.

OUTLINE OF STUDY

Loon Lake is situated near Clinton in the Interior plateau of British Columbia. The lake is about 8 miles (13 km) long and varies from one quarter to one half mile in width (Fig. 1). The main inlet enters at the east end of the lake while the outlet drains from the west end. Further geographical details of the

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area are given by Lindsey *et al.* (1959). Studies carried out from 1953 to 1955 by the British Columbia Game Commission (now Fish and Game Branch, Department of Recreation and Conservation) provided information on seasonal patterns of movement of trout into the inlet and outlet streams of Loon Lake. Almost all data on movement, size frequencies, sex ratios and mortality were obtained from the operation of fish traps, designed to capture fish moving upstream or downstream. Locations of traps and major spawning areas are shown in Fig. 1.

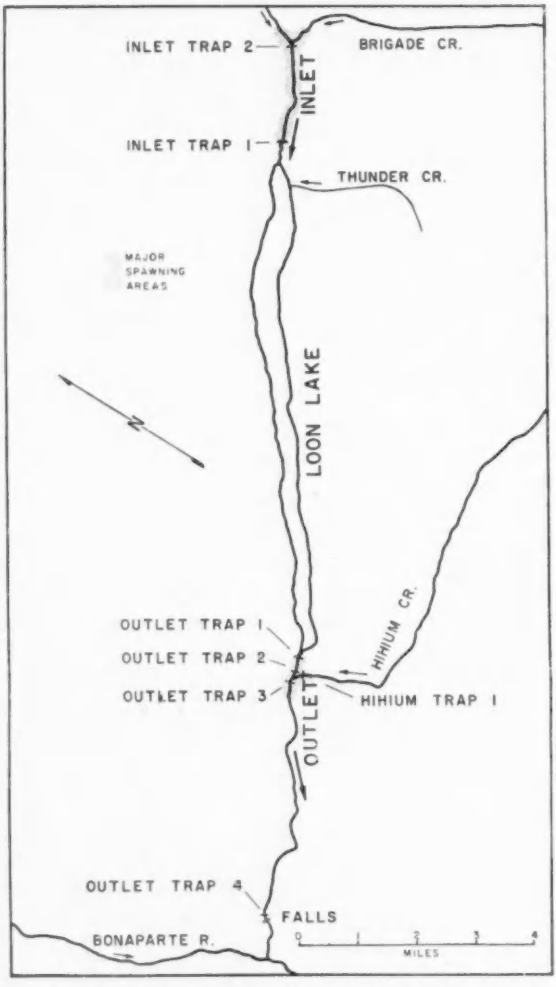

FIG. 1. Loon Lake stream system showing location of major spawning areas of rainbow trout and situation of traps.

Inlet Trap 1 was located about one-half mile (0.8 km) from the lake, below most of the suitable spawning areas in the inlet creek. Inlet Trap 2 was situated above most of the spawning gravel in the creek.

Outlet Trap 1 was located about 200 yards (184 m) below the lake. Only a small amount of spawning gravel occurred above the trap. Outlet Trap 2 was located about 1050 yards (975 m) below the lake; Outlet Trap 3 was situated below the junction of Loon Creek and Hihium Creek, 1300 yards (1200 m) from the lake. Outlet Trap 4, which only captured fish moving downstream, was placed about 4 miles (6.0 km) from the lake above falls impassable to upstream movement of fish. Hihium Trap 1 was placed on Hihium Creek about 70 yards (64 m) above its junction with Loon Creek.

The traps installed were of two types. Inlet Traps 1 and 2, and Outlet Traps 1, 2 and 3 each consisted of a diagonal screen fence with holding boxes at either end, modified from the design of Shetter (1938). Hihium Trap 1 and Outlet Trap 4 were modified Wolf-type traps (Wolf, 1951). Whenever stream conditions permitted, galvanized screen of 8 meshes per linear inch (3.2 per cm), was used on trap fences, boxes and leads. During high water coarse-mesh screen, $\frac{3}{4}$ inch (19 mm) square, was used.

Trap operation continued throughout the spawning season on both inlet and outlet creeks, from 1953 to 1955. About half of the spawners were examined in the inlet, where each year flooding conditions made operation of traps difficult. Outlet traps were easier to maintain and most fish entering or leaving the stream were recorded.

Outlet traps were usually serviced twice daily and inlet traps were usually checked once each day. During certain periods traps were checked 6 to 12 times daily for several days.

Fish which were captured in the traps were either tagged, fin-clipped or put through the trap unmarked; totals are shown in Table I. In 1953 aluminum chick wing tags (5 by 20 mm) were clipped on the dorsal side of the peduncles of the fish. In 1954 and 1955 celluloid Petersen disc tags, 13 mm in diameter, were pinned through the back of the fish a few millimetres anterior to the dorsal fin. During 1953 no spawners in the outlet or the inlet were marked by fin-clipping. In 1954, except for those fish marked with Petersen discs, most outlet spawners were marked only by removing the adipose fin. During the same period a number of fish, which had been marked as fingerlings by removing the left ventral fin in 1953, were recovered entering the outlet stream to spawn. These fish were re-marked by removing the adipose fin. In 1955 a number of fish at the outlet stream were captured and stripped of eggs or sperm for fish culture purposes. Such fish were marked by removal of the left pectoral fin.

All adult fish which were taken at the traps were handled with wet woollen gloves to reduce damage to the skin and scales. Most fish were measured (fork length) and scale samples were removed from some for age determination.

Daily stream temperature records were obtained by use of maximum and minimum thermometers or continuous temperature recorders. Stream levels were obtained at gauging stations near the traps in 1954 and 1955.

ENTRANCE INTO SPAWNING STREAMS

Outlet Creek

The seasonal movement of spawners into the outlet stream is shown on a weekly basis for 1953, 1954 and 1955 in Fig. 2. Information on numbers of trout taken between March 15 and April 30, 1953 was obtained largely from daily

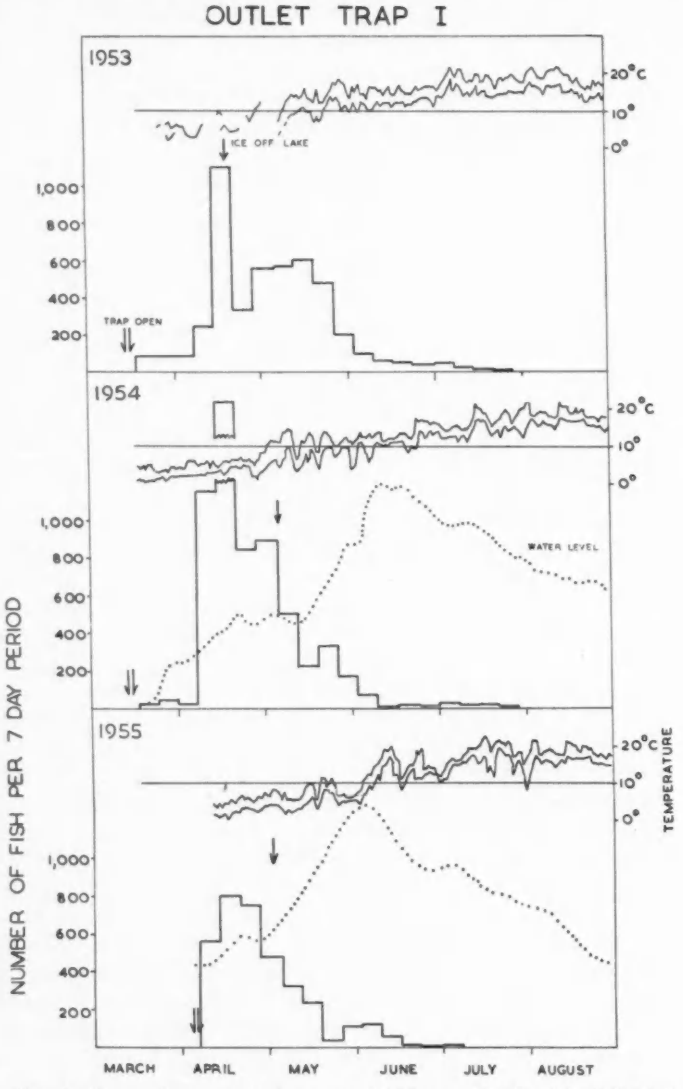

FIG. 2. Seasonal movement of spawners into Loon outlet Creek in 1953, 1954 and 1955. Water temperature lines indicate daily maximum and minimum.

records kept by hatchery personnel. No spawners were stripped during the remainder of 1953.

Stream water levels recorded at Outlet Trap 1 are not directly proportional to stream discharge, but are shown without scale in Fig. 2 as an indication of periods of low and high discharge. Records of water level shown in all figures are based on daily changes of readings with reference to a fixed level.

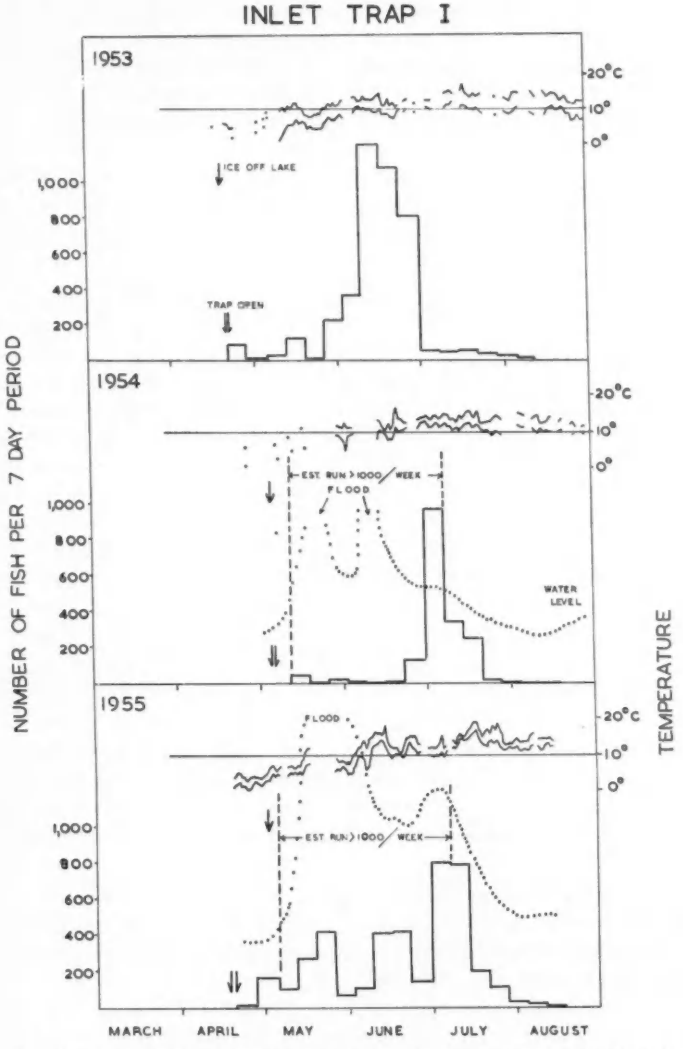

FIG. 3. Seasonal movement of spawners into Loon inlet Creek in 1953, 1954 and 1955. Water temperature lines indicate daily maximum and minimum.

Because Outlet Trap 1 was located slightly below the immediate exit of the outlet stream from Loon Lake (Fig. 1), the time when adult trout left the lake and entered the outlet could not be determined precisely. However, general seasonal characteristics of timing of the spawning run should not be obscured by short term delays which might be introduced in movement of trout from the creek mouth to Outlet Trap 1, a distance less than 1000 feet (305 m).

Mature adults first enter the outlet stream in mid March. At this time Loon Lake is still completely frozen over except for a small area of open water around the stream mouth. The outlet was surveyed for 1500 yards (1380 m) below its mouth (nearly all of the stream utilized for spawning) on March 19, 1954, 16 days before the ice left the lake. Only 43 mature adults were seen, 36 of which were in the upper 500 yards (460 m).

Few spawners appeared in the outlet stream until after the first week in April. A considerable increase in spawners taken at Outlet Trap 1 occurred during the second week of April in all years, with peak numbers recorded during the third week. This sudden influx of spawners to the outlet did not seem to bear any consistent relation to changes in physical conditions in the lake or outlet stream. An ice cover was present on the lake during the build-up phase of the spawning run in all years, and existed until well after the peak period of entrance in 1954 and 1955. During 1953 the ice cover broke up near the peak of the spawning migration (Fig. 2). Wind action or wind-generated currents could have no effect during that time (except possibly in the small patch of open water at the outlet). Stream water level and hence discharge increased steadily throughout the start, build-up, peak and declining phases of the outlet spawning run. Stream water temperatures ranged between 2.5 and 4.5°C during the sudden increase in number of outlet spawners. In 1954 the outlet temperature fluctuated little prior to, during and following the increase in the outlet run.

Maximum weekly catches of fish, in Outlet Trap 1, were taken shortly after the beginning of the run each year. The number of spawners moving downstream increased rapidly during the first two weeks of April, and the peak of the run occurred during the third week in April in all three years.

Largest numbers of fish moved into the outlet while creek temperatures ranged from 1 to 7°C. Later in the run considerable numbers of fish were taken while creek temperatures were as high as 15°C. A gradual increase in creek temperatures to 20°C appeared concurrent with the steady decline in number of trout moving downstream.

Figure 2 indicates that the bulk of the outlet run entered the stream during a period when water levels were rising. However, peak of the downstream spawning movement occurred about 6 or 7 weeks prior to the period when highest water levels in the creek were recorded.

Inlet Creek

Inlet Trap 1 was located approximately half a mile (0.7 km) upstream from the lake. Consequently data from it cannot be used to determine the period

during which fish entered the creek mouth. However, most of the spawning areas were located above the trap. Catches therefore indicated the time and duration of migration onto the spawning area.

Timing of movement of spawning fish through Inlet Trap 1 during 1953, 1954 and 1955 is shown in Fig. 3. Flooding conditions made it impossible to record the movement of all fish, but marking experiments indicated that about 20,000 fish went upstream through the inlet trap in 1954 and about 19,000 fish went through in 1955 (Lindsey *et al.*, 1959). Almost all of these fish moved through Inlet Trap 1 between May 5 and July 20 in 1954 and 1955. Temperature and water level data from 1953 to 1955 are fragmentary, but do allow general observations on environmental conditions during the run.

Spawners begin moving up the inlet creek while daily maximum water temperatures range from 3 to 9°C. Most of the run occurs while stream temperatures are from 5 to 15°C, and fish movement begins to fall off during periods of maximum stream temperature. The average summer temperature of the inlet is usually several degrees lower than that of the outlet. However, the inlet run is considerably later than that of the outlet and as a result most inlet spawners move upstream at temperatures higher than those at which downstream movement occurs in the outlet.

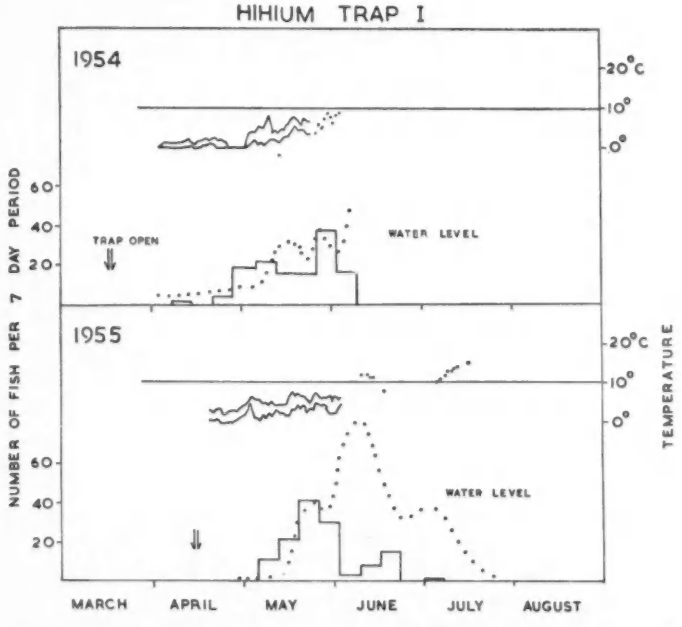

FIG. 4. Seasonal movement of spawners into Hihium Creek in 1954 and 1955. Water temperature lines indicate daily maximum and minimum; points in June and July show single daily readings. Due to flooding conditions, trap was partially or completely out of order during June and July in both years.

Some data on inlet water levels are available for 1954 and 1955. Apparently most fish move upstream during flood conditions in May and June.

Hihium Creek

Each year some spawners which had moved down the outlet creek turned up Hihium Creek and were taken in Hihium Trap 1 (Fig. 1).

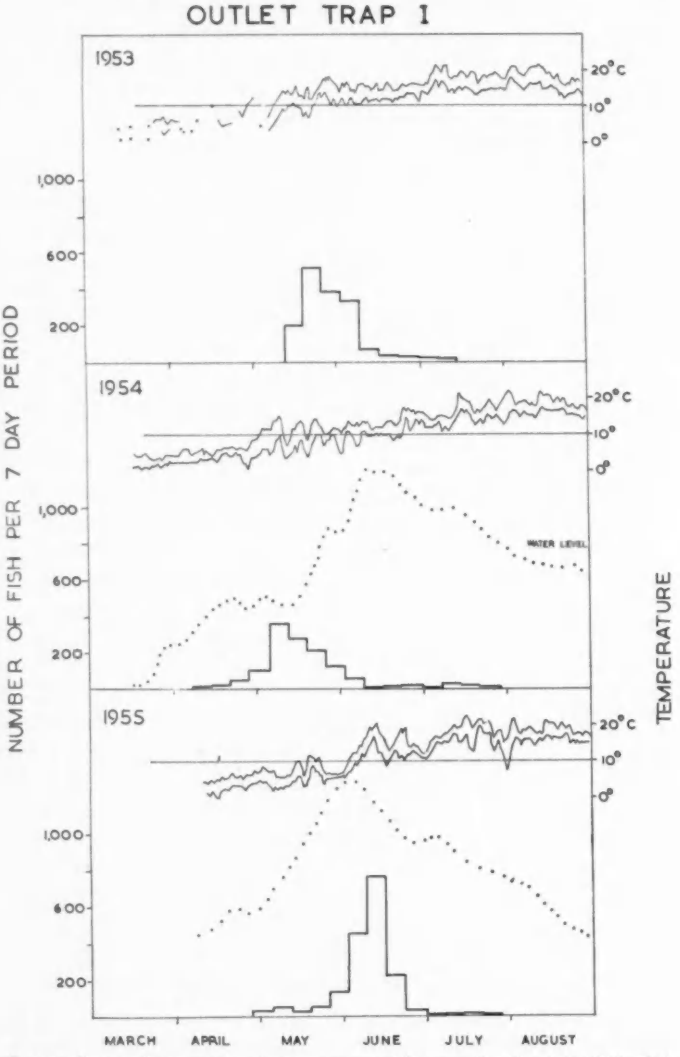

FIG. 5. Seasonal movement of spawners out of Loon outlet Creek in 1953, 1954 and 1955. Water temperature lines indicate daily maximum and minimum.

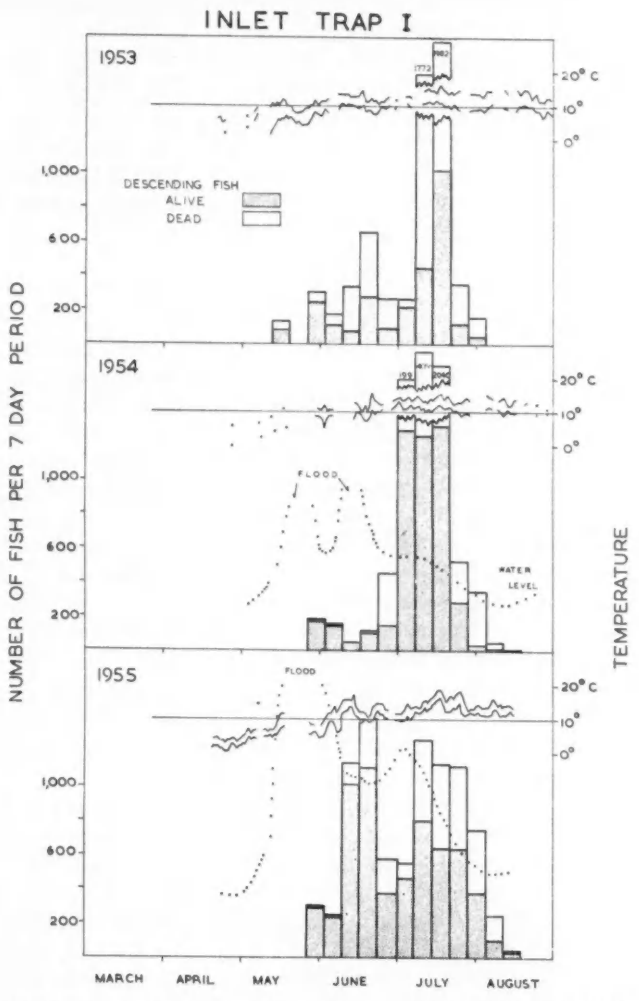

FIG 6. Seasonal movement of spawners out of Loon inlet Creek in 1953, 1954 and 1955. Water temperature lines indicate daily maximum and minimum; numbers given above some bars indicate number of dead fish in that 7 day period.

In April 1954 a few spawners entered Hihium Creek while daily maximum water temperatures ranged from 1 to 2°C (Fig. 4). During 1955 spawners were first taken in creek temperatures of 4 to 7°C. Most of the fish trapped were migrating at low stream temperatures.

Trap installations in Hihium Creek were completely removed by freshets in 1954 and no fish were recorded after June 4. In 1955 flooding conditions made it impossible to capture all ascenders, but some fish were taken throughout the high water period when creek temperatures were as high as 15.5°C.

Increasing numbers of spawners began moving up Hihium Creek when the downstream migration in Loon outlet was declining. At this time water temperatures of Hihium Creek were at least 4°C lower than Loon outlet Creek. Movement up Hihium Creek increased with rising temperatures and water levels.

EXIT FROM SPAWNING STREAMS

Outlet Creek

At the outlet, spent fish left the creek during May and June each year (Fig. 5). Time elapsed between the peaks of movement into and out of the outlet stream was 22 days in 1954 and 51 days in 1955. Figure 5 suggests that fish begin to leave the outlet stream when daily temperature maxima pass the 10°C line. Although the fish showed a tendency to leave the creek when water temperature maxima rose above 10°C it is noteworthy that the upstream surge of fish also occurred during and following a rapid rise in creek temperature. It is therefore not clear whether exodus from the outlet occurs as a result of change of temperature or as a result of water temperature having reached a critical level. In any event water temperature conditions may affect length of stay in creek by determining time of upstream migration.

Differences in length of stay in creek bore no direct relation to differences in stream level during the three years. Length of stay in the creek however, does appear to be inversely related to number of fish spawning, as shown later in Table V.

Three plots are presented in Fig. 7 showing relation of length of time spent in the creek to date of entrance. During 1954 and 1955 fish entering earlier remained in the creek much longer than those entering at the end of the run. During 1953 fish were tagged only late in the run. The time spent in the outlet was somewhat longer for fish tagged late in the 1953 spawning season than for those in comparable periods tagged in 1954 and 1955 spawning seasons. Fish tagged while entering the stream in 1955 remained longer than did those in 1954.

Inlet Creek

Spent fish in the inlet began to move back downstream during the peak of spring floods (about three weeks to one month after they entered the stream) (Fig. 6). Most of the exodus from the stream occurred while water levels were receding during late June and July. Apparently most spent inlet fish moved downstream after temperatures had reached 10°C.

Figure 7 shows that, like outlet spawners, fish entering the inlet creek early in the spawning season in 1954 remained in the stream longer than those entering later.

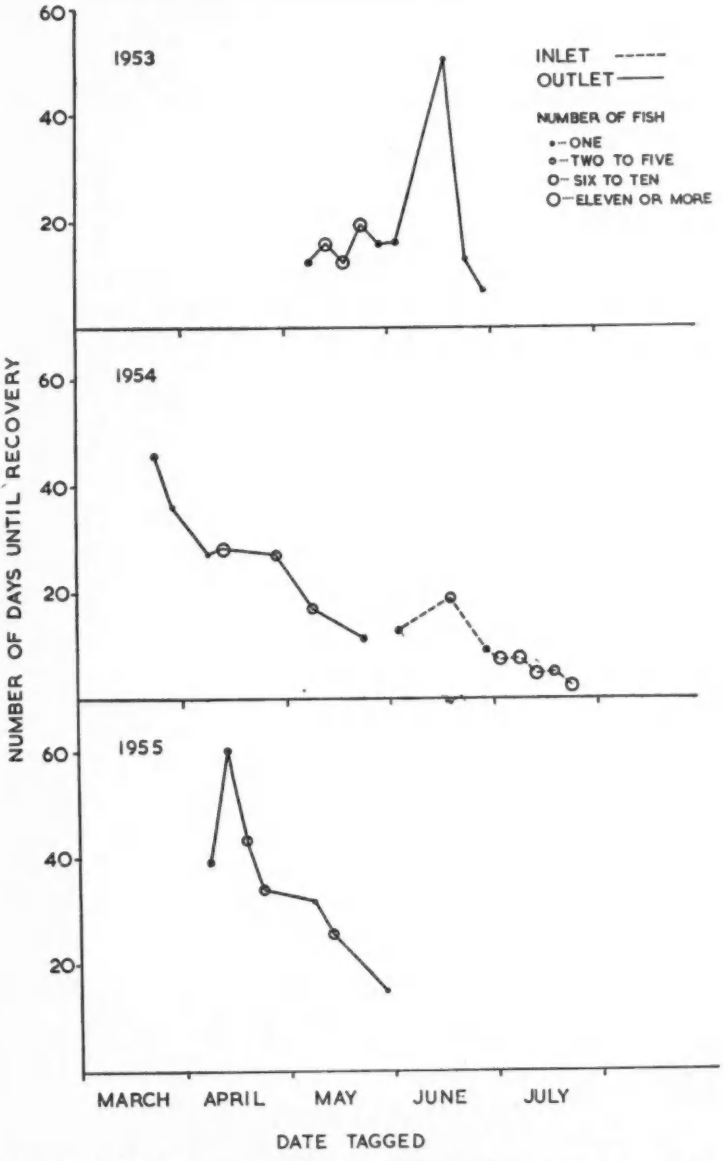

FIG. 7. Relation between time of entrance into spawning stream (date tagged at Trap 1) and time of return to lake (days until recovery at Trap 1) for spawners at Loon inlet and outlet Creeks.

DIEL VARIATIONS IN MOVEMENT WITHIN STREAMS

Outlet Creek

Diel variation in movement of spawners and spent fish was recorded at the outlet traps during short periods of May in 1954 and 1955 (Fig. 8). There is some indication that downstream movement reached two daily peaks, one of which coincided roughly with the daily maximum in stream temperature. The two peaks were not always well defined and did not always occur at the same time on successive days. Separate plots (not shown) of movement of males, unripe,

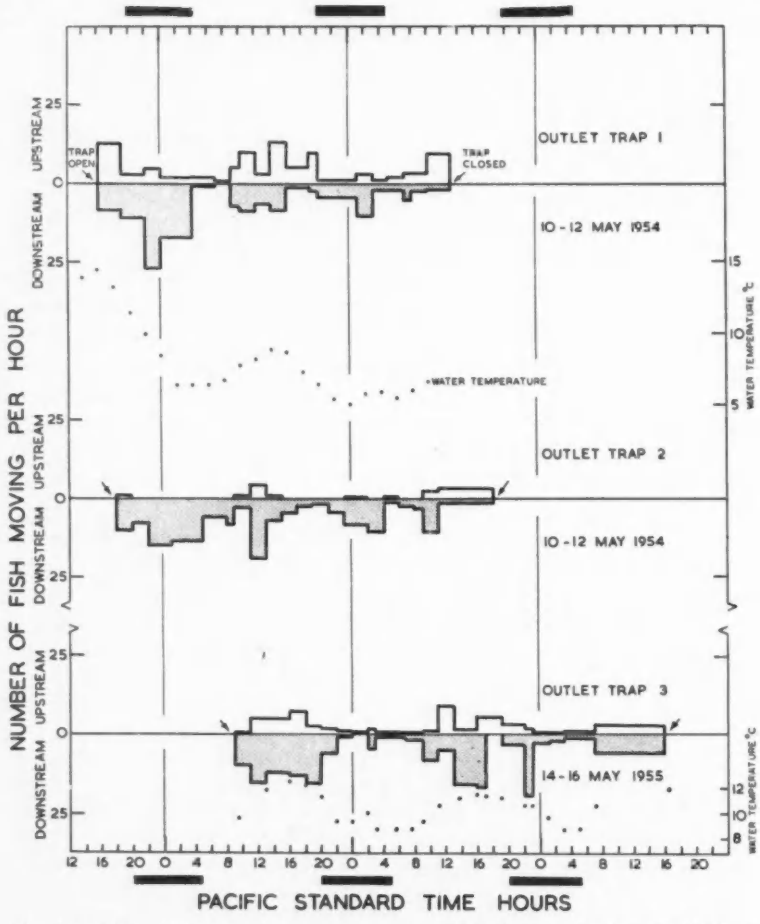

FIG. 8. Diel variation in movement of spawners within Loon outlet Creek in 1954 and 1955; shaded bars indicate fish entering creek, open bars indicate fish leaving creek, black horizontal bars indicate approximate period of darkness.

ripe, and spent females indicated that the diel pattern of downstream movement was similar for the two sexes and for females in different spawning conditions.

The movement of spent ascenders, shown in Fig. 8, occurred primarily during the day, and coincided with the daylight peak of downstream movement, and with the daily temperature peak.

Inlet Creek

Figure 9 shows diel variations in movement of spawners during three periods in 1954 and 1955.

Most spawners moved up the inlet creek between 1200 and 1800 hours each day. Very few ascenders were recorded during hours of darkness in any of the periods considered. Although fish tended to move upstream each day during the period when water temperature was rising, no obvious relationship was noted between daily temperature maxima and daily totals of ascending spawners.

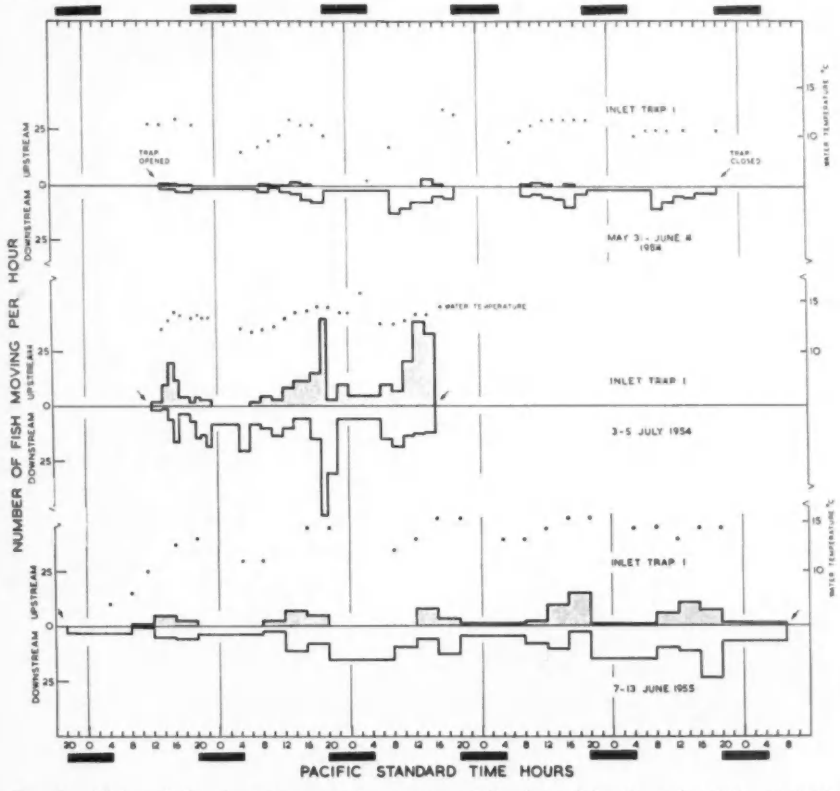

FIG. 9. Diel variation in movement of spawners within Loon inlet Creek in 1954 and 1955; shaded bars indicate fish entering creek, open bars indicate fish leaving creek, solid horizontal bars indicate approximate period of darkness.

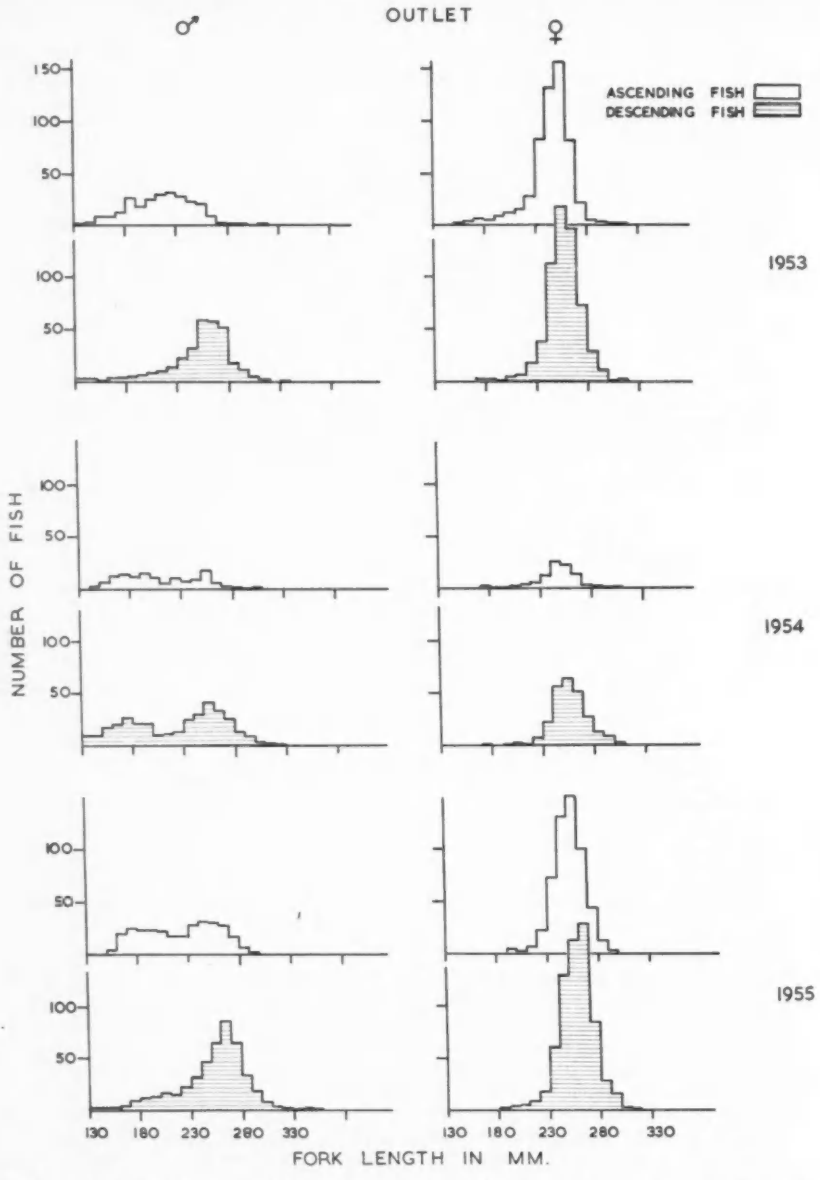

FIG. 10. Length–frequency distribution of male and female spawners entering (descending) and leaving (ascending) Loon outlet Creek in 1953, 1954 and 1955.

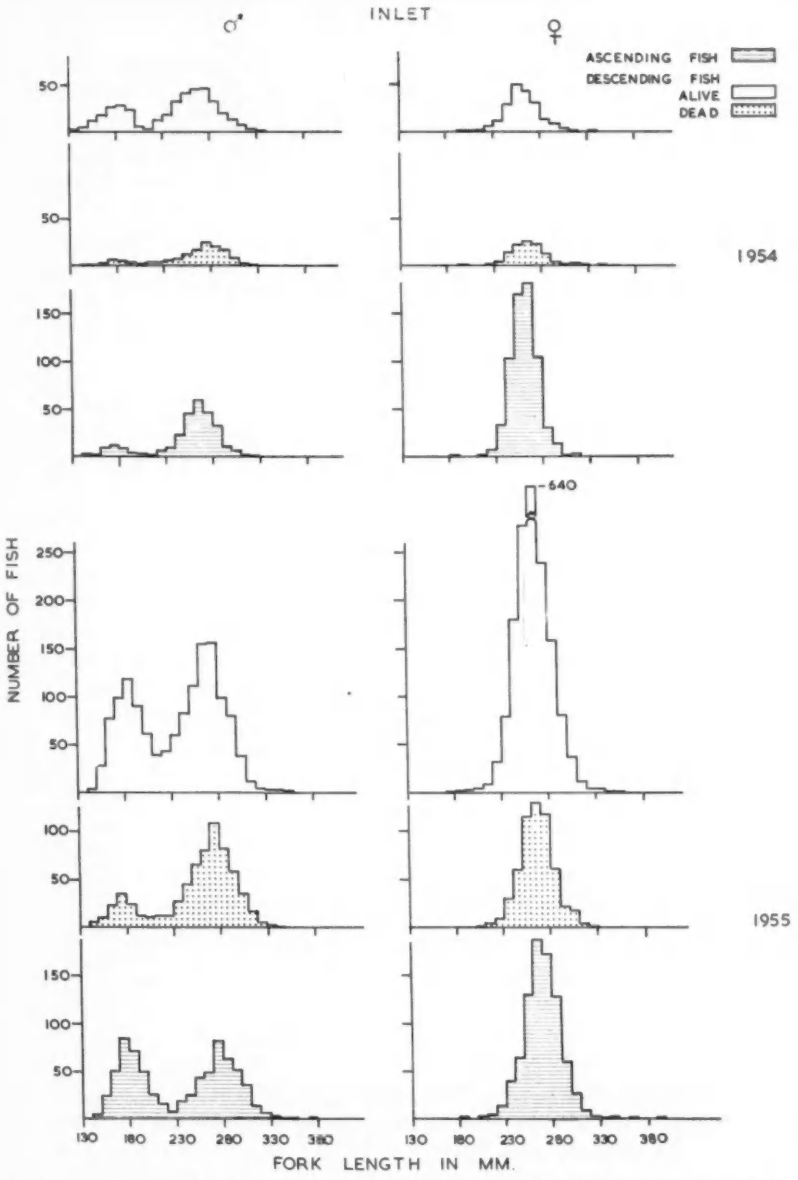

FIG. 11. Length–frequency distribution of male and female spawners entering (ascending) and leaving (descending) Loon inlet Creek in 1954 and 1955.

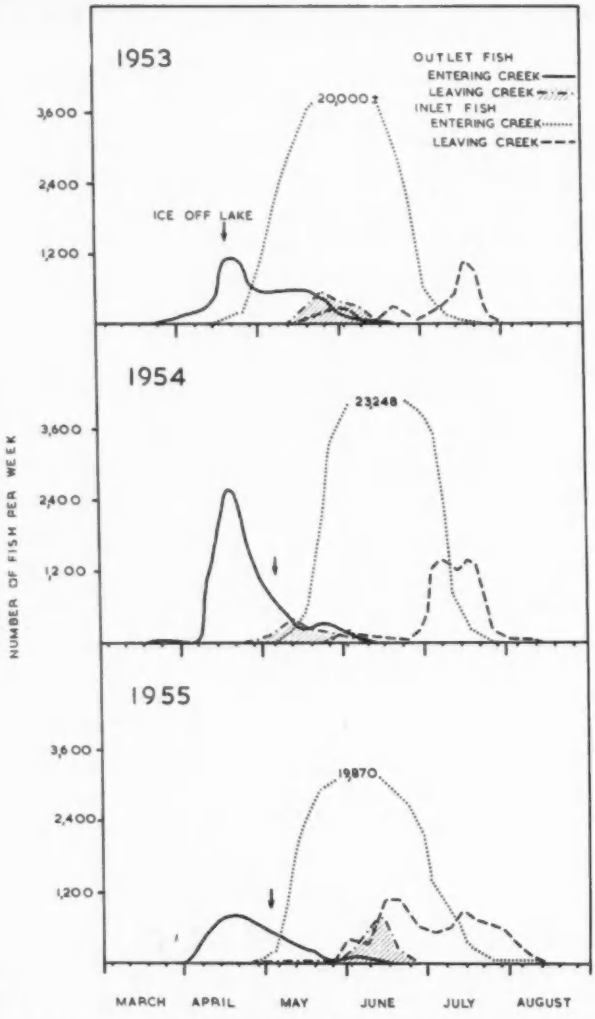

FIG. 12. Summarized presentation of entrance and exit of spawners at Loon outlet and inlet Creeks in 1953, 1954 and 1955.

Descending fish showed no consistent diel pattern of movement. For example, between May 31 and June 4, 1954 almost all descenders moved during the daylight periods while during July 3, 4 and 5, 1954, large numbers of spent fish moved downstream at night as well as during day. Between July 7 and 13, 1955, fish moved downstream at all periods of the day, with no obvious relation to changes in light intensity.

SIZE OF SPAWNERS

Figure 10 shows length-frequencies of male and female spawners and spent fish in the outlet creek from 1953 to 1955. Similar length frequencies are given in Fig. 11 for fish spawning in the inlet. In addition to spent live fish recovered descending in the inlet, a large number of dead fish were taken each day. Such fish were recovered either as carcasses that drifted down or as fish that died in the trap. In Fig. 11 dead fish are plotted separately from live descenders.

Not all fish in the runs were measured, but size frequency plots represent a large sample of each run. Two size groups of males occur in both the inlet and outlet run each year. Relative numbers in each size group fluctuate from year to year and between inlet and outlet. Variations in relative numbers of large and small males may indicate changes in year class strength, as was shown for Paul Lake (Larkin *et al.*, 1950). One size group and probably one age group dominates each spawning run of female trout. (Age could not be determined reliably from scale reading due to complicated life history patterns of fish originating from inlet and outlet streams.) Slight differences are apparent, from year to year, in average length of fish in the spawning runs. In 1955 the average lengths of large male spawners (in size groups over 215 mm fork length) and of female spawners were greater than in corresponding groups in 1953 and 1954. Male and female inlet spawners in most modal groups were 10 mm longer than those in comparable modal groups in the outlet run in 1954 and 1955. No obvious differences occurred in the size of small male spawners, under 215 mm fork length, in the two streams in either year. Apparent differences in the relative numbers of large and small males entering and leaving the creeks will be discussed in a subsequent section dealing with spawning survival.

SEX RATIOS

Relative numbers of females, large males and small males during the runs at the inlet and outlet were compared, using data for the years 1954 and 1955. For purposes of this comparison each spawning run was arbitrarily divided into three sections; a middle component which included the peak and the main body of the run, and early and late components which included the build-up and declining phases of the run.

Outlet Creek

During 1954, the ratio of males to females was nearly 1 to 1 during the early and late parts of the run. During the peak of the run, however, approximately 85% of the fish were males and most of these were small fish (under 215 mm fork length).

During 1955 males constituted about 54% of the outlet run during its early phase but at the peak of the run the proportion of males had dropped to 44% and during the last portion of the run it fell to 33%.

Inlet Creek

During 1954 the inlet run consisted of about 70% females, 25% large males and 5% small males. Relative numbers of males and females were the same at the peak and late stages of the run. Data were inadequate to make valid comparisons involving the first period of the run.

The 1955 inlet run consisted of males and females in a nearly 1 to 1 ratio during all three periods. However, the proportion of small males to large males was considerably higher at the peak of the run than it was during either the early or late phases.

The relative numbers of females, large males and small males not only varied in the three phases of any particular run but also showed marked differences at both inlet and outlet streams during the years studied. No consistent picture of sex ratio or relative numbers of large and small males can be drawn for the two spawning seasons considered. Furthermore, sex ratio during the three phases of the outlet run bore no relation to that of the inlet run during the same year. In a given year, relative numbers of large and small males during the three phases of the run were not the same at the inlet and outlet.

Although the sex ratio varied during different phases of the run, both sexes began to move into the spawning stream at about the same time. The increase, peak and the decline of the male spawning run paralleled that of the female run. Considering the inlet and outlet separately, spent males and females returned to the lake at about the same time.

SPAWNING SURVIVAL

Estimates of survival of outlet spawners based on fin-clipped, tagged and unmarked fish were available for the years 1953, 1954 and 1955. Survival of fish in the outlet stream is equated to recovery of spent fish leaving the stream. While there is evidence, presented elsewhere in the text, that some spawners overwinter in the stream, the numbers of fish doing so are not considered to be great enough to invalidate conclusions drawn by relating recovery and survival.

Survival of inlet spawners could not be obtained for the same period because of difficulty in trap operation. In addition, fish drifting downstream in the inlet were often in very poor condition and although many of these entered the traps alive a further undetermined number died before reaching the lake. Therefore recovery of fish entering the inlet traps could not be equated to survival.

Table I gives the number and percentage of unmarked, clipped and tagged fish surviving the 1953, 1954 and 1955 runs in the Outlet Creek. Survival data are not given on all categories or marks for all years because some types of tags and marks were used only for one or two seasons.

Unmarked

During two years some fish were put downstream unmarked. Examination of the number of unmarked fish returning gives a measure of survival of this group. Survival of unmarked fish was high during 1953 and 1955. During

1954 no unmarked fish were put downstream but in spite of this 396 unmarked ascenders were recorded. This figure may be comprised of fish which remained in the stream over winter, or of fish which escaped downstream unrecorded through the outlet trap, or of both. (Contribution of fish from Hihium Lake was known to be negligible). Because Outlet Trap 1 operated efficiently in 1954, the former group probably predominated. Although trap losses and overwintering in the creek may cause some error in calculations of survival of unmarked fish, it is nevertheless apparent that unmarked outlet spawners have a relatively high survival. If one subtracts 396 fish (the number unaccounted for in 1954) from the number of spent ascenders in the outlet in 1953 and 1955, the survival is still over 30% in 1953 and over 50% in 1955.

Adipose Removed

In 1954, 6625 descending fish were marked by the removal of the adipose fin at Outlet Trap 1. Of these 1431 were subsequently tagged at and passed down through Outlet Trap 2. Therefore in calculating the survival of fish marked only by adipose clipping, 5194 fish (6625 minus 1431) will be considered. Of these 779 (or 15%) returned to the lake.

In 1955, 110 adipose-clipped fish moved down into the outlet trap from the lake. These fish, which were spawning a second time, had been marked in the outlet the previous year. A total of 77 adipose-marked fish were recovered as ascenders in 1955. The survival of fish in this group appears high. As in the case of unmarked fish, the high recovery of adipose clipped fish may be due in part to fish escaping unrecorded through the fence and in part to overwintering in the stream. Moreover, the 1954 survival of adipose-clipped fish (15%) is not directly comparable to that in 1955 (70%) because the latter group had had a year to recover from clipping, and also represented a select group of fish which had survived an additional year.

Left Ventral Plus Adipose Removed

In 1953 two-year-old fingerlings entering the lake from the outlet were marked by removal of the left ventral fin. During the 1954 spawning run 198 fish from this group were recovered descending through Outlet Trap 1 and were marked again by removal of the adipose fin. Of these, 27 (or 14%) survived to re-enter the lake.

Left Pectoral Removed

In 1955, 386 fish were stripped of eggs or sperm by hatchery staff and passed downstream. These fish were marked by removal of the left pectoral fin. Survival of this group of fish to re-enter the lake was 9%.

Tagged with Chick Wing Tags

In 1953 about one-third of the outlet spawning run was tagged with chick wing tags. Of 1436 fish so marked, 105 or 7% survived with tags attached and returned through Outlet Trap 1.

Tagged with Petersen Discs

During 1954 and 1955 a portion of the spawning run was marked using Petersen disc tags. Table I shows that survival of these fish was 5% in 1954, and 8% in 1955.

Adipose Removed and Fish Subsequently Tagged

Of those fish adipose-clipped and passed downstream through Outlet Trap 1, 1431 were taken subsequently at Outlet Trap 2, where they were tagged with Petersen discs and put downstream. Only 2% of these were recovered later moving into the lake through Outlet Trap 1. The additional handling and tagging probably accounted for the very low survival of fish in this group (see Table I).

Table I. Spawning survival of unmarked, clipped and tagged fish, at Outlet Trap 1, in Loon Creek during 1953, 1954 and 1955.

A. Number of fish released below Outlet Trap 1.
B. Number of spent fish recovered entering Outlet Trap 1.
C. Percentage of fish recovered.
LV— left ventral removed, Ad — adipose fin removed,
LP— left pectoral fin removed.

	1953			1954			1955		
Fins removed and tags applied	A	B	C	A	B	C	A	B	C
	No.	*No.*	*%*	*No.*	*No.*	*%*	*No.*	*No.*	*%*
Unmarked	3157	1384	44		396		2001	1589	79
Ad				5194	779	15	110	77	70
LV+Ad				198	27	14			
LP[a]							386	35	9
Chick tag	1436	105	7						
Petersen tag				1048	56	5	690	55	8
Ad + Petersen tag[b]				1431	35	2			
Total	4593	1489	32	7871	1293	16	3185	1812	57

[a]Fish stripped of eggs and milt before marking.
[b]Adipose fin removed at Outlet Trap I, fish tagged at Outlet Trap II.

Total Survival

The bottom line of Table I gives the survival of the whole run for three consecutive years, considering all fish, marked and unmarked, together. If the years are ranked in ascending order of the total number of spawners (3185 in 1955, 4593 in 1953, 7871 in 1954) they are found to be in descending order of survival (57, 32 and 16% respectively). Trap records give no suggestion that a disproportionately high number of fish passed the trap unrecorded in 1953 and 1955. High overall mortality in 1954 cannot be attributed to tagging, because although losses were highest in 1954 a smaller fraction of the run was tagged than in 1953 or 1955. Neither can high mortality in 1954 be due to disproportionate size or sex ratios, because the run in that year included a large number of small males which are shown later to be subject to a relatively low mortality.

Independent evidence on the effect of population density in different years is available from records kept each year on the condition of almost all spent fish ascending through Outlet Trap 1. Using subjective criteria, each fish was recorded as being in good or poor condition, depending on the degree of injury and fungus infection (Table II).

Table II. Number of spawners entering and leaving Outlet Trap 1 and the percentage of the latter in poor condition.

Year	Entering	Leaving	Poor condition
	No.	*No.*	*%*
1953	4593	1489	23
1954	7871	1258	30
1955	3185	1812	20

During these years higher numbers of fish on the spawning ground were accompanied by a higher percentage of fish leaving the grounds in poor condition. Moreover, absolute number of fish returning to the lake is lowest in the year when total number of spawners had been highest.

Data on condition of spent fish, on survival of tagged fish and on survival of the whole outlet spawning population strongly indicate that survival of spawning fish in the outlet is inversely correlated with total number of spawners. No marked differences in stream levels or temperatures were observed which might account for varying mortalities.

Differences in Survival of Males and Females

A comparison of returns of males and females adipose clipped in the outlet indicates a higher survival of female fish. In 1954, 2596 females were put downstream onto the outlet spawning grounds. Of these 450, or 17%, returned to the lake. During the same period 329, or only 13%, of the 2531 males returned to the lake. There was no significant difference in survival between males and females marked with tags and recovered during the same period at the outlet. A total of 537 females were tagged and 28, or 5%, were recovered; 511 males were tagged and 28, or 5%, were recovered.

Survival of Fish of Different Sizes

Comparison of length frequencies of ripe and spent fish taken in Outlet Trap 1 revealed that large females suffered a higher mortality than small ones. This comparison was based only on fish which were marked (by adipose removal) at Outlet Trap 1 in 1954 and recovered during the same season. Results are therefore not biased by the addition of ascenders that may have entered the spawning area unrecorded or remained in the creek all winter. The mean fork length of female spawners moving into the outlet (253.6 mm) was significantly greater than that of spent fish returning to the lake (242.8 mm) ($P<0.01$).

The spawning run of male fish, unlike that of the females, consisted of large numbers of both 3 and 4 year old fish. A chi-square test showed that there was a significant difference ($P<0.01$) in spawning mortality between "small" males (215 mm and under) and "large" males (over 215 mm). Large males (mostly 4 years old) suffered a considerably higher mortality than small ones (mostly 3 years old). Table III summarizes data on spawning mortality of "large" and "small" fish, marked by removal of adipose fin, which entered the outlet stream in 1954.

Table III. Spawning mortality in different size groups of male and female trout. Fish were marked by adipose removal while entering the outlet creek in 1954, and were enumerated as they left again.

Size, mm	Female		Male			
	255 and less	>255	170 and less	171–215	216–255	>255
Number entering	259	252	145	143	212	168
Number leaving	82	24	39	54	52	8
Mortality, %	68.3	90.5	73.1	62.2	75.5	95.2

Figures 10 and 11, showing length frequencies of samples of fish entering and leaving inlet and outlet streams during 1953, 1954 and 1955, indicate that heavier mortality among larger fish is a phenomenon common to both streams.

Summary of Outlet Survival

(1) Higher survival occurred among unmarked fish than among those that were tagged or clipped.

(2) Higher survival occurred among clipped fish than tagged fish.

(3) Survival of spawners was inversely correlated with numbers of fish entering spawning stream.

(4) The percentage of spawners leaving the creek in poor physical condition was highest in years when greatest numbers of fish entered the creek.

(5) Survival of female fish was higher than that of males.

(6) Large male and female fish suffered a higher mortality than small fish.

DISCUSSION

Seasonal Movement of Spawners

Figure 12 summarizes movements of fish into and out of inlet and outlet creeks for the years 1953–1955. Curves are based on weekly numbers of fish and were drawn by smoothing points on bar diagrams in Figures 2, 3, 5 and 6.

The peak of the spawning run to the outlet creek occurred at approximately the same time each year despite considerable differences in time of disappearance of ice from the lake (and accompanying differences in stream temperature). On the other hand the spawning run to the inlet creek was appreciably later when melting of the ice was delayed. Inlet spawners characteristically entered the spawning stream 3 to 5 weeks later than the outlet fish, at temperatures which were on the average several centigrade degrees higher. Inlet fish spent a shorter average time in the stream before returning to the lake. As has been mentioned previously, annual variations occurred in length of time spawners remained in the outlet creek; these may be related to stream temperature or spawning population density or both.

Most studies dealing with the mechanics of stream entrance by spawning rainbow and cutthroat trout have been concerned primarily with the entrance of fish into inlet streams (Mottley, 1933, 1938; Rayner, 1942; Cope, 1956). Little attention has been given to the study of trout which migrate into the outlets of lakes to spawn. Yet spawning in both inlet and outlet occurs in a number of British Columbia lakes in addition to Loon Lake (e.g., Pennask, Knouff and Pinantan Lakes). In each of these lakes and in Wasilla Lake, Alaska (Whitesel *et al.*, 1957) the outlet run begins earlier than the inlet run.

In instances where a species of fish is represented by several genetically distinct races in a given system, (e.g. races of sockeye salmon in the Fraser River system) variations in seasonal timing of spawning may be accounted for by genetically controlled variations in life cycles of races which are adjusted to conditions of a specific stream. At Loon Lake and probably in other British Columbia lakes where inlet and outlet spawning occurs, the fish apparently have not evolved into distinct races. A high percentage of rainbow trout in Loon Lake have been shown to home to the streams where they were hatched (Lindsey *et al.*, 1959), but too much straying occurs to allow the build-up of two genetically distinct races. If the racial hypothesis for the two spawning populations of trout in Loon Lake is untenable, there arises the problem of explaining on some other basis the occurrence of the regular differences in seasonal timing of spawning migrations which have been outlined.

Although it is beyond the scope of the data to describe exact time of movement into the creeks, or limnological conditions of the lake at the onset of spawning migrations, a number of major differences between inlet and outlet spawning runs can be demonstrated. Furthermore, information on time of entrance into the streams and time of disappearance of ice cover allow a consideration of some factors which have been discussed previously (Mottley, 1938; Rayner, 1942) in connection with spawning migrations of trout.

Differences in time of entrance of spawners to inlet and outlet streams demonstrate that the two spawning runs are not initiated by any single factor such as day length, rise in lake temperature above a critical point, or disappearance of ice cover. Spawners begin moving into the outlet creek before the ice cover leaves the lake, at a period when lake temperature is near its minimum. Most fish move down the outlet creek while temperatures are low but increasing gradually. Figure 2 shows that in 1953 a large proportion of the run of fish to the outlet creek occurred after the ice left the lake. In 1954 and 1955, on the other hand, most fish entered the creek before ice cover on the lake broke up. It seems unlikely that lake temperature changes or disappearance of ice cover alone are causal agents in initiation of the outlet run.

Movement of spawning fish into the inlet, however, occurs after disappearance of ice and during periods when creek temperatures are increasing. Obviously in Loon Lake no single environmental change is responsible for the onset of movement into both inlet and outlet creeks.

Mottley (1938) states that onset of the main portion of the run of rainbow trout to Paul Creek (an inlet tributary to Paul Lake) occurs following warming of the creek and lake. Daily numbers of fish entering Paul Creek appeared to increase during periods of onshore wind action. Temperature data available for Loon Lake and Loon inlet Creek suggest that the run occurs under creek and lake temperature conditions similar to those in Paul Lake. At Skaneateles Lake, New York, the main run of rainbow trout entering an inlet creek migrates at temperatures between 5.5 and 12.8°C (Rayner, 1942). Rayner suggests that increased flow of roiled water into the lake may serve as an orienting factor. Similarly the main run of fish entering the inlet of Loon Lake does so while the creek is in flood. The circumstances under which fish enter the inlet of Loon Lake do not appear very different from those described for Skaneateles Lake or Paul Lake.

Fish entering the outlet do so under an entirely different set of circumstances from those associated with inlet migration. Most fish move down the outlet while days are shorter, ice still covers the lake, creek temperatures are low and relatively stable, and creek discharge is low.

The hypothesis that fish returning to home streams recognize certain features of the environment (Lindsey *et al.*, 1959) still does not explain why outlet fish move down the outlet to spawn 3 to 5 weeks before movement to the inlet occurs. The outlet stream tends to warm sooner than the inlet, hence any spawning movements which are tuned to stream temperature patterns might be expected sooner in the outlet. However, it has been pointed out that outlet spawners move downstream and spawn earlier in the season than inlet fish, at lower creek temperatures. Migration into the two streams is therefore probably not initiated at a given threshold temperature.

The inlet stream becomes free of ice and may be open for a considerable period before fish enter it. It seems unlikely that a mechanical barrier such as ice blockage on the inlet stream is responsible for the delay of fish entrance.

Spawning migrations of trout may be initiated by one set of factors (e.g. photoperiod, age of fish, or seasonal changes in conditions of lake or streams) and may be modified subsequently by other conditions (e.g. wind action in lake, stream temperature, or stream discharge). An adequate explanation of mechanisms resulting in different timing of the inlet and outlet runs cannot be given. However, the following suggestions are offered, in speculation, as to the type of mechanism which may produce differences in timing of runs into the two streams.

In early spring all fish in the lake have had a similar light and temperature history over at least the previous 6–8 months. As a result, most fish destined to spawn in a given year may reach the same condition of sexual development at the same period. Fish homing to either stream do so by recognizing certain features of the stream mouth. Fish moving down the outlet take part in a migration involving less activity than that of inlet fish. Inlet fish are required to swim actively into the current to reach the spawning areas; outlet fish are not required to do this. Sullivan (1953) and Brett (1958) have shown that fish are able to swim more rapidly at higher temperatures. This being the case, at low temperatures fish may be sufficiently active to move downstream with the current in the outlet but may not swim upstream against the current in the inlet. Inlet and outlet fish may both recognize areas around their home stream at the same period and congregate in these areas prior to entrance into the stream. Although large numbers of fish congregate near the mouth of the inlet stream, upstream movement may not be started until water temperature rises to a level several degrees higher than that at which the run to the outlet can commence.

Spawners which move down Loon outlet Creek and then ascend Hihium Creek do not conform to the foregoing hypothesis. They are, however, in a much more advanced state of ripeness than fish ascending the inlet creek at the same time, which may account for their swimming upstream at somewhat lower temperatures.

Diel Movement of Spawners

Various animals display regular daily peaks in feeding, movement or other activities. Movement of adult trout over a 24-hour period in the inlet and outlet creeks of Loon Lake follows a cyclic pattern. Activity is apparently related to changes in temperature and light intensity (Table IV).

Movement of spawning fish into the outlet differs from movement into the inlet in that outlet fish tend to show two daily periods of activity, while upstream movement of inlet spawners occurs in a single period of activity during daylight hours. Movement of spent fish from the two streams is quite different, in that spent outlet fish move in a regular daily pattern. These fish must be in good condition in order to swim upstream to reach the lake. The explanation of the irregular pattern of downstream movement in the inlet may lie in the effect of current on the spent fish. Spent fish in good condition may show periodic changes in activity. However, many spent inlet fish are in poor condition and often are unable to maintain position in the current when they reach the trap. Perhaps

they are displaced out of the relatively still water by the ripe, stronger fish and are carried downstream by the current. In such a situation fish might drift down to the trap over a period of many hours, regardless of light or temperature, after large numbers of ripe fish have moved upstream.

Outlet spawners, unlike inlet fish, apparently move toward spawning areas principally during two periods each day. Because the two peaks of downstream movement occur at times when light and temperature conditions are different, it is difficult to understand what role these factors play. Peaks of downstream

TABLE IV. Summary of diel movement of fish in outlet and inlet creeks.

Stream	Direction of movement	Movement of fish	
		Day	Night
Outlet	Ripe fish downstream	Peak during daily temperature maximum	Second peak of movement after dark
	Spent fish upstream	Peak during daily temperature maximum	Reduced movement
Inlet	Spent fish downstream	No regular pattern	No regular pattern
	Ripe fish upstream	Peak during daily temperature maximum	Reduced movement

movement occurring during daylight may be related to stream temperature maxima. (Upstream movements of inlet spawners and spent outlet fish coincide with temperature maxima). Downstream movement in the outlet during darkness, however, occurred sometimes with falling and sometimes with rising stream temperatures. A more detailed study is required to elucidate the bimodality of spawning migration in the outlet creek.

SURVIVAL OF SPAWNERS

The fish marking at Loon Lake gives good evidence that the type of mark and amount of handling a fish receives has a great effect on its chances of survival. During the 3 year study fish were given treatments ranging from simple handling and passing downstream to tagging plus fin-clipping.

Groups of fish that were unmarked showed a very high survival (30-50%). Clipped fish showed about a 15% survival. When fish were tagged, or when they were stripped and fin-clipped by hatchery personnel, survival rate was lower still, ranging from 5 to 9%. Fish that were clipped, tagged and handled 3 times or more showed a very low survival of 2%.

Judging from these results, if it is not possible to count total numbers of fish entering and leaving a stream, clipping of the adipose fin probably gives the best method of calculating survival of the marking methods used here.

In the outlet creek of Loon Lake a striking relationship exists between numbers of fish, survival of spent fish, condition of spent fish and length of time spent in the stream (Table V).

During years of high spawner density, increased mortality and reduced time spent in the stream result from increased activity among spawners. In greater concentrations, the amount of social stimulation may be greater, fish may mate and spawn more rapidly. Moreover, ripe fish may tend to displace spent fish quickly from choice sites, resulting in their more hasty return to the lake. The accompanying poorer condition of fish returning lakeward may be attributable to increased fighting under more crowded conditions.

Data on the total production of the outlet for the years 1953 to 1955 are not available. It is therefore not possible to determine the relation between spawners and production of young. However, numbers of fry moving up to the lake were higher in 1953 (4593 spawners) than in 1954 (7871 spawners). Since a large fraction of each year's production in the outlet remains in the stream over winter, the figures on fry production must be taken with reservations in any consideration of total production.

Marked changes in year-class strength, observable in anglers' catches as well as in spawning runs, may be attributable not only to environmental conditions but also to differences in spawning efficiency suggested by the foregoing data.

TABLE V. Survival, time spent in the outlet creek (time between peak of movement into and out of creek), and the condition of the surviving spawners leaving the creek, and numbers of fry leaving the creek each year. Data ranked according to the number of fish entering the stream.

	Spawners	Survival	Time in Creek	Fish leaving in poor condition	Fry
	No.	*%*	*Days*	*%*	*No.*
1954	7871	16	22	30	3727
1953	4593	32	30	23	6778
1955	3185	57	51	20	–

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Migratory Behaviour of Juvenile Rainbow Trout, *Salmo gairdneri*, in Outlet and Inlet Streams of Loon Lake, British Columbia[1,2]

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ABSTRACT

The marked differences in response to water current, exhibited by juvenile rainbow trout migrating into Loon Lake from its outlet and inlet streams, were studied both in the field and in experimental laboratory apparatus. All available evidence argued against genetically discrete outlet and inlet stocks, each maintaining different innate responses to water current. Difference in water temperature between streams was shown, in field and laboratory experiments, to regulate direction of juvenile trout migration through action on behaviour associated with downstream movement, maintenance of position and upstream movement.

In laboratory experiments with cool (5 and 10°C) flowing water, recently emerged fry rarely made contact with the stream bottom in darkness and exhibited much more downstream movement than in warm (>14°C) water. In cool streams of the Loon Lake system (daily mean consistently <13°C) large numbers of recently emerged fry moved downstream in darkness. Laboratory experiments indicated that combination of cool water (10°C) and long day length (16 hours) induced downstream movement of fingerlings. In the field, fingerlings moved downstream largely in late spring and summer in cool streams of the Loon Lake system.

In laboratory experiments with warm (15 and 20°C) flowing water, recently emerged fry made frequent contact with the stream bottom in darkness and exhibited much less downstream movement than in cool (10°C) water. In the warm outlet stream (daily mean in summer usually >15°C) recently emerged fry maintained position in darkness. Laboratory experiments suggested that short day length (8 hours) may facilitate maintenance of position exhibited by fingerlings in streams during late autumn and winter.

Upstream movement of fry recorded in the field and tested in the laboratory was most pronounced in warm water (>14°C). Fingerlings subjected to rapid 5-degree (C) increases in water temperature in an experimental stream exhibited an immediate increase in upstream movement. Upstream movement in summer of large fry and fingerlings occurred only in the warm outlet stream; daily periodicity of upstream movement was positively correlated with sharp rises in water temperature.

Evidence examined from four other widely separated stream systems indicated an environmental control of migration in juvenile rainbow trout similar to that demonstrated in the Loon Lake stream system. Possible mechanisms and interaction of factors controlling migratory patterns between and within streams are discussed. Significance of the predominant role played by temperature is considered.

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INTRODUCTION

THE PHENOMENON of migration — large-scale movement of animals from one place of habitat to another at some reasonably well-defined stage in their life history — has intrigued early naturalists (Bertin, 1956) and has claimed attention of zoologists in many fields, particularly since the turn of the century. Spectacular, long range migrations exhibited by such diadromous fishes as eels and salmon have received a good portion of this interest (Fontaine, 1954). Less attention has been devoted to equally challenging but less dramatic migration of fish strictly within fresh water (Hoar, 1953). Moreover it has been customary to think of many fish migrations, even in freshwater species, as an active upstream movement of maturing adults towards a spawning site and a more or less passive downstream transport of young and surviving adults (Russell, 1937). Few studies have been carried out on a species, some of whose adults in one lake system migrate *up* inlet streams and others *down* an outlet stream at spawning time, and whose young in order to take up lake residence must at some stage move *downstream* from one hatching site and *upstream* from the other.

Rainbow trout are known to spawn both in the outlet and inlet streams of several lakes in British Columbia. Mottley (1931a) noted the occurrence of inlet and outlet spawning trout at Pinantan Lake near Kamloops. Lindsey *et al* (1959) have studied homing of trout to inlet and outlet spawning streams at Loon Lake. Spawning trout have been trapped for fish-cultural purposes by the British Columbia Fish and Game Branch on both outlet and inlet streams of several other lakes, such as Pennask and Knouff. Rainbow trout spawning runs are known to occur in outlet and inlet streams of Wasilla Lake in Alaska.

The phenomenon of fish spawning both in an outlet and inlet of one lake is not limited to rainbow trout. Such migratory behaviour may occur in brown trout, *Salmo trutta* (Lake Rensjöån and other Swedish lakes — Runnström 1952), in cutthroat-rainbow hybrids, and in grayling, *Thymallus arcticus* (Grebe Lake, Wyoming — Kruse, 1959), sockeye salmon, *Oncorhynchus nerka* (Owikeno Lake, B.C.— Foskett, 1958; Babine Lake, B.C.— Johnson, 1958), white suckers, *Catostomus commersoni* (Cluculz Lake, B.C.— Geen, MS, 1958) and in longnose suckers, *C. catostomus* (Bouchie Lake, B.C.— Geen, MS, 1958).

The mechanism whereby the juveniles move upstream or downstream, as the case may be, to enter the lake has only rarely been considered. Runnström (1952) mentions the upstream and downstream migration of juvenile brown trout in Lake Rensjöån, and notes the behaviour problem created by this phenomenon. Rounsefell (1958) points out that the factors determining lakeward movement of sockeye fry which emerge in outlet and inlet streams of lakes are not yet understood. Regardless of the details of their migratory behaviour, juveniles in outlet and inlet streams must at some stage exhibit directly opposite responses to water current in order to enter the lake. One of the fundamental problems, then, in a study of migratory behaviour in situations as outlined above, is to determine the mechanism which operates to produce such marked differences in behaviour between young of the same species.

Two explanations can be postulated: (1) *genetically distinct* outlet and inlet stocks, each maintaining appropriate innate behaviour responses which result in movement of young into the lake; (2) *genetically similar* outlet and inlet stocks responding to environmental differences between the streams which produce appropriate current responses and other behaviour characteristics resulting in movement of young into the lake.

Maintenance of genetically distinct stocks from each stream would demand an extremely high degree of homing of adults from the lake, unless the majority of young resulting from straying individuals were either lost from the system or prevented in some way from reproduction with homing fish. Lindsey *et al* (1959) have reviewed the possibility of genetically distinct groups of trout existing in Loon Lake. As a result of (a) recovery of marked adult strays spawning in a non-parental stream, (b) calculations of probable fractions of homing and straying fish in inlet and outlet average annual spawning populations, and (c) transfer experiments with adult spawners, they concluded that the available evidence argued against genetically discrete inlet and outlet spawning stocks.

Inlet *and* outlet spawning populations of rainbow trout have rapidly become established in some formerly barren lakes in British Columbia which probably were stocked with progeny reared from eggs collected at only *one* type of stream (personal communication from F. Pells, retired hatchery supervisor, British Columbia Fish and Game Branch). As far as is known, young entered these lakes both from inlet and outlet streams. Spawning populations were maintained in both types of stream for some time after original stocking. If the response to current on the part of young trout from inlet and outlet spawning stocks were largely innate and distinct in each type, then rapid establishment of both types from planting of one stock would not have been expected.

The alternate postulate is that there are genetically similar inlet and outlet stocks whose current responses are controlled largely by environmental differences between inlet and outlet streams. That no marked genetic differences may exist between inlet and outlet stocks does not, of course, imply that differential response to water current does not involve innate behaviour patterns. As Hoar (1958) has pointed out, fixed innate patterns of behaviour in fish are usually oriented or directed by a variety of environmental factors. At different intensities of a single factor or under combinations of several factors, marked alteration in behaviour response can be expected. For example, reactions of young fish to light and to water current can be greatly changed or even reversed at different levels of illumination or of current speed, or following sudden changes of temperature (Andrews, 1946; Keenleyside and Hoar, 1954).

A study of juvenile rainbow trout migration was undertaken to obtain data both from field conditions and from controlled experiments in the laboratory which would permit critical examination of environmental control of behaviour differences in migration of young fish from outlet and inlet streams of the same lake.

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LOON LAKE STREAM SYSTEM

A. Geography of the Area

Loon Lake is situated in a narrow valley at an elevation of 2820 feet about 12 miles (19.3 km) east of Clinton on the southern interior plateau of British Columbia. The lake is approximately 8 miles (13 km) in length and varies between one quarter and one half mile (0.4 — 0.8 km) in width. The shores drop off steeply to a depth exceeding 100 feet (30 m) along most of the length of the lake; maximum depth is 213 feet (65 m).

The principal inlet stream enters the northeast end of the lake, draining Upper Loon Lake, about 6 miles (10 km) to the northeast, and small lakes and marshes to the southeast (Fig. 1). This will be called *Inlet Creek*. Other very small inlet streams enter the lake, but most of these do not flow permanently. *Outlet Creek*, draining the southwest end of Loon Lake, maintains a fairly level gradient to a point about 1000 yards (910 m) below the lake, where it is joined by Hihium Creek draining Hihium Lake some 8 miles (13 km) to the east. Below this junction the outlet gradient increases until it drops over a series of rapids and waterfalls impassable to upstream movement of fish, about 4 miles (6.5 km) from the lake.

Rainbow trout, native to Loon Lake and the only species of fish present, spawn in both its inlet and outlet streams. In Inlet Creek the spawning area begins about one-half mile (0.8 km) above the lake (Fig. 1), near the site of Inlet Trap 1, and extends for over a mile upstream beyond this point. In Outlet Creek the majority of spawning takes place in the first 1000 yards (910 m) below the lake, although some fish spawn in Hihium Creek above its confluence with the outlet, and in the outlet below this junction. Movement of fish between Loon Lake and either Hihium Lake or Upper Loon Lake is probably rare and of negligible importance in this study.

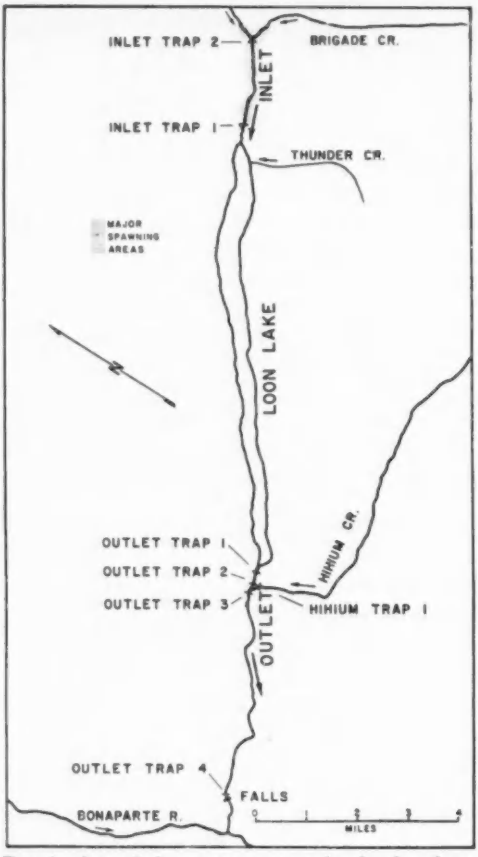

FIG. 1. Loon Lake stream system showing location of major spawning areas of rainbow trout and situation of traps.

B. PHYSICAL AND CHEMICAL FEATURES

1. WATER TEMPERATURE (expressed in Centigrade degrees throughout this paper).

Daily maximum and minimum water temperatures are compared in Fig. 2 for Outlet, Inlet and Hihium Creeks. During most of the spring and throughout summer in 1953 and 1954 Outlet temperatures, both maximum and minimum, were consistently higher than those in either Inlet or Hihium Creek. In both 1953 and 1954 (Fig. 2), maximum temperature of Inlet and Hihium Creek rarely exceeded 15° whereas Outlet Creek was usually well above 15° and frequently higher than 20° during most of late spring and summer. Similar differences in temperature (not shown) occurred between these streams during other periods of study in 1955, 1957 and 1958.

Figure 2 suggests another difference between Outlet Creek on one hand and Inlet and Hihium Creek on the other. More rapid and extensive fluctuations in temperature (both in daily maxima and minima) are evident in late spring and summer at Outlet Creek than appear either at Inlet or Hihium Creeks. A detailed comparison of interdiurnal (day to day) variability in maximum temperature between streams in the Loon Lake system showed Outlet temperatures to be significantly more variable ($P < 0.01$) than those at Inlet or Hihium

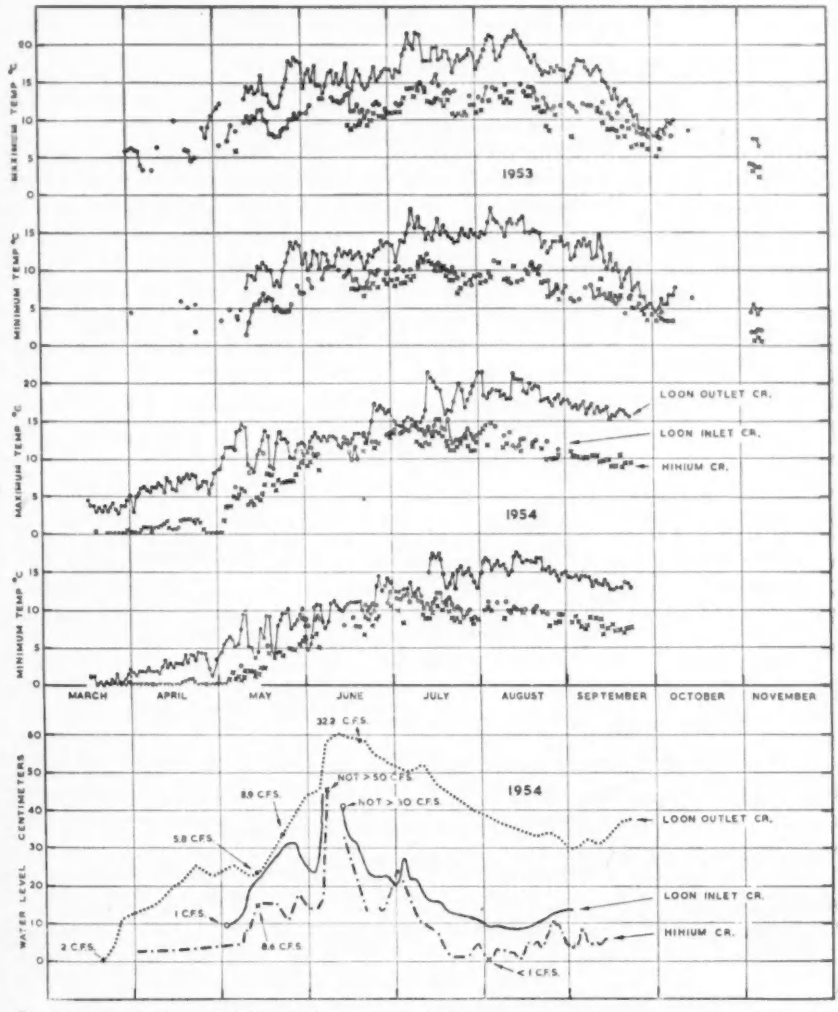

FIG. 2. Comparison of daily maximum and minimum stream temperatures and water level at Inlet, Outlet and Hihium Creeks.

Creeks during late spring and summer. Data by Hofstetter (1953) show that interdiurnal variability of water temperature of several Austrian lake surfaces and outlets is much greater during the period April–September than for October–March. Unfortunately no comparison was made between inlet and outlet streams of these lakes.

Little change in temperature was noted along the length of Outlet Creek between the lake and the entrance of Hihium Creek or along most of Inlet Creek. A substantial drop in temperature of the outlet occurred below the confluence of Hihium Creek at most times during spring and summer seasons.

2. Water Level and Discharge

Stream water levels and available data on discharge are given for 1954 in Fig. 2. Water levels shown cannot be compared directly (cf. discharge and level at Outlet Creek and Hihium Creek on May 13), but they do illustrate seasonal changes between streams. Daily water levels were not recorded during most of the 1953 season. Apart from the absence of excessively high levels in June, the seasonal pattern in 1953 water level was similar to that shown for 1954. All streams have maximum annual level and discharge in June, the month of maximum rainfall in the section of the central interior plateau around Loon Lake (Chapman, 1952), with minimum discharge during winter and early spring. Hihium Creek showed the most violent fluctuations ranging from flood levels near 50 cubic feet per second to less than 1 (1.4–0.03 m^3/sec). Although water level (and discharge) in Outlet Creek is not subject to such rapid and extreme fluctuation as evident both for Inlet Creek and Hihium Creek, nevertheless seasonal changes in discharge are similar in the three streams.

3. Water Quality

Analyses of water samples from Outlet, Inlet and Hihium Creeks showed appreciable differences in total dissolved solid content between the streams. Inlet Creek had the highest dissolved solid content, ranging between 400 and 500 parts per million (ppm). Hihium Creek was consistently lowest in dissolved solids (118–156 ppm) while Outlet Creek was intermediate (293–392 ppm).

C. Biological Features

1. Invertebrate Fauna

Although no extensive study was made of the invertebrates of Outlet, Inlet or Hihium Creeks, differences in this fraction of their fauna became apparent after cursory examination of the streams and a limited amount of sampling.

In the first few hundred metres below Loon Lake, plankters and gammarids, probably originating from the lake, add substantially to the fauna of the outlet stream. These have largely disappeared where the outlet is joined by Hihium Creek and are not well represented in the latter nor in Inlet Creek. The outlet stream also supports a rich "indigenous" fauna with caddis and simulid larvae particularily abundant between the lake and the entrance of Hihium Creek.

Hihium Creek probably supports a much lower abundance of invertebrates than does Outlet Creek. Caddis, simulid and other larval and nymphal stages of insects are much less abundant than in the outlet stream. Excessive fluctuation in stream level and scouring of the bottom during flash floods characteristic of Hihium Creek may result in a reduced invertebrate fauna.

Abundance of invertebrates in Inlet Creek probably is intermediate between that of Outlet and Hihium Creeks. Gammarids were not found in any bottom or stream (floating material) samples nor in any stomachs of 125 trout fry[3] examined from Inlet Creek in 1953 (Hartman, MS 1954).

2. Young Trout Density

The average size of spawning populations of trout is markedly different between Outlet, Inlet and Hihium Creeks. Each year about 5000 trout spawn in Outlet, about 22,000 in Inlet and only a few hundred in Hihium Creek (Lindsey *et al.*, 1959). Consequently far more fry emerge each year in Inlet creek than in Outlet or Hihium Creeks. However since the inlet has a more extensive spawning area (Fig. 1) it is a moot point whether or not concentrations of fry per unit section of stream are actually higher in Inlet than in Outlet creek. In *localized* areas of Inlet Creek counts of fry along sections of stream edge were somewhat higher than in similar areas at Outlet Creek. Concentrations of fry in Hihium Creek were noticeably lower than either Inlet or Outlet Creeks.

METHODS AND APPARATUS

A. Field Studies

1. Operation of Traps

Most of the information on movement of young rainbow trout in streams of the Loon Lake system was obtained by operation of traps designed to catch and hold fish of all sizes moving either upstream or downstream. Location of traps in the system is shown in Fig. 1; all of these except Outlet Trap 4 retained fish moving in either direction. Inlet and Outlet Traps 1 and 2 were essentially diagonal screen fences with leads and holding boxes at each end, modified from the design of Shetter (1938). Hihium Trap 1 and Outlet Trap 4 were modified Wolf type traps (Wolf, 1951). During most periods of operation, traps were fitted with 8 mesh/linear inch (3.2 mm square) regalvanized hardware cloth which retained virtually all fry. Occasionally during high stream discharge $\frac{3}{8}$ and $\frac{3}{4}$ inch (9.5 and 19.0 mm) square mesh screening was used on traps in order to record movement of fingerlings under freshet conditions.

Traps were attended at least every other day and usually, during periods of considerable movement, every day. Young trout moving either upstream or downstream were counted and returned to the stream either above or below the fence depending on their direction of movement as indicated by capture in the two-way traps. Periodically, samples of young trout were preserved in

[3]Two groups of juvenile trout were distinguished in outlet and inlet streams of Loon Lake (a) *fry* or young in their first calendar year of existence and (b) *fingerlings* or young in their second or later calendar years.

10% formalin solution for later examination. All fingerlings and some fry moving through each trap were marked by removing portions of either right or left ventral fins. A distinctive fin clip was used at each trap. Although all fry moving upstream through Outlet Traps 1 and 2 were fin-clipped, only a small portion of those moving downstream through Inlet Traps 1 and 2 were marked, as the majority of these were too small for effective removal of fins. Lindsey *et al.* (1959) have given details of juvenile trout marking in streams of the Loon Lake system.

In addition to use of traps, some information on movement of young trout was obtained by observation of fish crossing standards strips placed in the stream bottom at right angles to the direction of flow.

2. Records of Environmental Conditions

Water temperature was recorded by use of continuous temperature recorders (Negretti & Zambra and Weksler) or maximum-minimum weather thermometers. The standard recording station on Outlet Creek was located approximately 810 feet (247 m) downstream from the lake, between Outlet Traps 1 and 2 (Fig. 1). Periodically other records were also obtained at each trap site on the outlet stream. Water temperature was recorded at each of the traps on Inlet Creek and at the trap on Hihium Creek.

Stream level was recorded on metre sticks firmly anchored into the stream bed at each trap site. Estimation of discharge was obtained by recording water velocity with a Leupold & Stevens Current Meter No. 111 across stream sections.

Measurement of light intensity during the day was made with a Photovolt Model 200 photometer calibrated directly in foot-candles. Intensities of nocturnal illumination were determined by a Photovolt Model 514 M photometer fitted with phototube C and a scotopic (human eye) correction filter. Divisions on the photometric scale of Model 514 M photometer with and without scotopic filter were calibrated against those on Model 200 photometer in order to express low intensity readings in *very approximate* foot-candle units. Shifts in spectral characteristics of light from dusk to dawn make use of foot-candle units for recording nocturnal illumination questionable.

3. Nocturnal Observation

Nocturnal behaviour of young rainbow trout in streams of the Loon Lake system was observed by use of infra-red viewing apparatus. An infra-red viewer (AN/SAR-4) and field power supply was used for all field and most laboratory observations in darkness. War surplus infra-red lamps (Models X-264) operated from 6V car batteries were used as a source of infra-red light. The infra-red viewer, flanked on each side with an infra-red lamp, was mounted on a "Star D" swivel head tripod stand to provide a unit convenient for field use.

Experiments conducted by Duncan (1956) yielded no evidence that young coho salmon could detect or were affected by infra-red radiation. No responses of young rainbow trout were noted, either in streams at Loon Lake or in the laboratory, which suggested that these fish were affected by use of the infra-red viewing apparatus.

4. Experimental Flumes

Two galvanized metal rectangular troughs (20 × 25 × 244 cm) were used at the confluence of Outlet Creek and Hihium Creek to study responses of young trout to water currents at different temperatures.

A small wing dam was constructed across Outlet Creek and water was led along a wooden flume to a point on Hihium Creek a few feet upstream from its junction with Outlet Creek. In this way a sufficient head was available to operate the two experimental flumes side by side, one supplied from a head tank with Outlet Creek water, the other with Hihium Creek water. Both galvanized iron flumes (painted inside with hatchery black asphaltum) were placed at a slight incline to create a flow of water over a series of baffles along their length and into a Wolf-type trap at their downstream end. Baffles divided each flume into five equal sized compartments plus one small compartment screened off at the upper end where water from each head tank was introduced. Height of baffles and incline of flumes were adjusted to allow a drop in water level of about 2 cm between each compartment. Flow into each flume was adjusted by a gate on the head tank supplying its water. Discharge through both flumes was maintained at 57 l/min during all experiments.

B. Laboratory Studies

Two basic units of apparatus were used in laboratory experiments to test responses of young trout in flowing water. The experimental chamber, constructed at the Department of Zoology, Cambridge, England, was utilized primarily for studies on activity, vertical distribution, and bottom contact of fry. Current responses of fry and fingerlings were studied in the experimental stream, built at the Zoology Department, University of British Columbia.

1. Experimental Chamber

The experimental chamber consisted of a glass-sided tank in which a pumping system maintained a controllable flow of water at velocities up to 10 cm/sec (Fig. 3A). Water was drawn off at one end of the tank and led into a temperature control basin before going to a pump and recirculating to the tank. Water temperature was controlled thermostatically with heating and cooling coils immersed in the control basin. Upon entering the glass tank, water passed through baffles which reduced turbulence. Perforated screens were installed in the tank, forming a chamber 30 cm in length, 18 cm in width and 16 cm in depth (Fig. 3A). The bottom of the chamber was covered with gravel, giving fry the opportunity to avoid direct flow present in the chamber. The glass tank was enclosed in a darkroom where illumination could be maintained at desired intensities. Infra-red viewing apparatus was used to observe fish in darkness.

2. Experimental Stream

Response of young trout to water current was studied in a continuous flume 50.8 cm wide, 35.6 cm deep and 9.7 m in circumference (measured at middle of channel) which extended around the perimeter of a room (Fig. 3B).

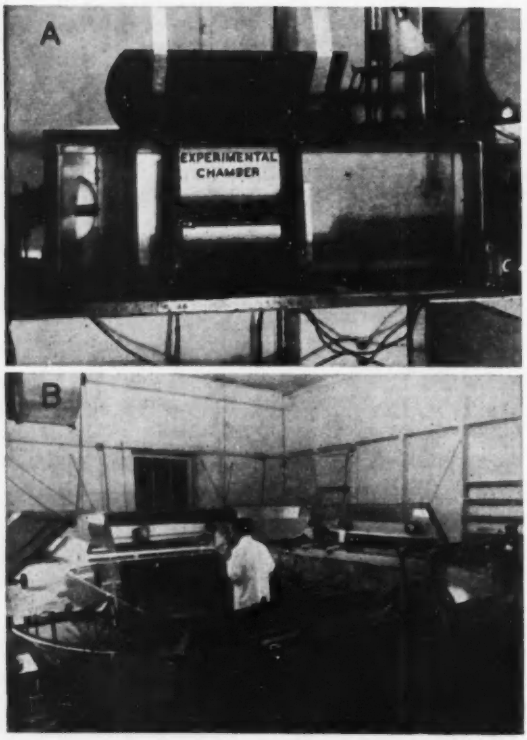

FIG. 3. Laboratory apparatus used to study movement of juvenile trout in flowing water under various temperature and light conditions. **A.** Experimental chamber. **B.** Experimental stream.

Light intensity was controlled either by a Type 116 "Powerstat" in circuit with "Lumiline" incandescent lamps suspended on viewing mirrors overhanging the stream, or by an iris diaphragm on an incandescent lamp housing which reflected light off the ceiling. Water temperature was controlled thermostatically by heating and cooling coils in one section of the channel. At a water depth of 15 cm a current with a maximum velocity approaching 20 cm/sec (mean cross-sectional velocity of about 8 cm/sec) could be maintained in the stream channel by a screened double pumping system. Higher or lower water velocities could be maintained by alteration of water level, regulation of valves on the pumping system or operation of only one or both pumping units.

OUTLINE OF MIGRATORY BEHAVIOUR

Any description, however brief, of the migratory behaviour of juvenile rainbow trout in the Loon Lake stream system immediately becomes concerned

with three streams, two age-groups of young fish, downstream and upstream movement, diel[4] and seasonal patterns of movement, annual changes in some features of migration, as well as maintenance of position in streams by certain ages of young. Therefore it is essential to have a general picture of migration before details of young trout behaviour in any one situation may be appreciated. Tables I and II present in summary fashion major features of the migratory

[4]Diel refers to the 24-hour period of a day and a night.

TABLE I. Summarized comparison of major features of migratory behaviour of rainbow trout fry in Outlet, Inlet and Hihium Creeks.

Outlet Creek	Inlet Creek	Hihium Creek
No extensive period of downstream movement of fry following emergence.	Extended period of downstream movement following emergence.	Extended period of downstream movement following emergence.
Downstream movement, when occurring, takes place almost entirely at night.	Downstream movement takes place almost entirely at night.	Downstream movement takes place almost entirely at night.
Majority of fry maintain position within restricted areas of stream during both day and night for first few weeks after emergence.	Majority of fry maintain position in streams only during daylight.	Majority of fry maintain position in streams only during daylight.
After spending first few weeks following emergence within restricted locality in stream, many fry begin an active upstream migration towards and into lake during daylight hours. This movement begins in early July and ceases in late September or early October.	No appreciable upstream movement shown by fry at any time.	No appreciable upstream movement shown by fry at any time.
Many fry remain in stream over winter, entering lake as fingerlings the following spring.	Most fry enter lake between July and September; few successfully over-winter in stream.	Most fry leave creek between July and September; few successfully over-winter in stream.

TABLE II. Summarized comparison of major features of migratory behaviour of rainbow trout fingerlings in Outlet, Inlet and Hihium Creeks.

Outlet Creek	Inlet Creek	Hihium Creek
Many fingerlings remaining in stream in early spring.	Very few fingerlings remaining in stream in early spring.	Few fingerlings remaining in stream in early spring.
No appreciable downstream fingerling movement recorded at any period of the year.	Sporadic periods of downstream fingerling movement in mid-summer.	Sporadic periods of downstream fingerling movement in mid-summer.
Well-defined period of upstream movement during spring and early summer.	No definite period of upstream movement; occasional days on which a few individuals moved upstream.	No appreciable upstream movement at any time.
Majority of fingerlings move upstream only during hours of daylight.	Few fingerlings which move upstream, do so largely during daylight hours.	

behaviour of young trout in the Loon Lake stream system. Data supporting many of the statements and generalizations will be found in later sections.

DOWNSTREAM MOVEMENT OF FRY

A. Characteristics of Downstream Movement

1. Seasonal periodicity

Movement of fry down streams of the Loon Lake system is summarized for the 1953 season in Fig. 4. Apart from the June period at Outlet Creek, no marked annual changes in seasonal periodicity of downstream fry movement in the 3 streams were evident on other years (1954, 1957, 1958). Similar patterns of downstream movement in 1953 appeared at both locations on Inlet Creek (Inlet Traps 1 and 2) and at 3 locations on Outlet Creek (Outlet Traps 1, 2, and 4; Outlet Trap 3 was not operated with fine screen during most of the season). As Hihium Trap 1 sampled between 25 to 75% of the stream discharge during most of the 1953 season, the fry total given for that trap in Fig. 4 probably represents somewhat more than one-quarter of the total number of descending fry.

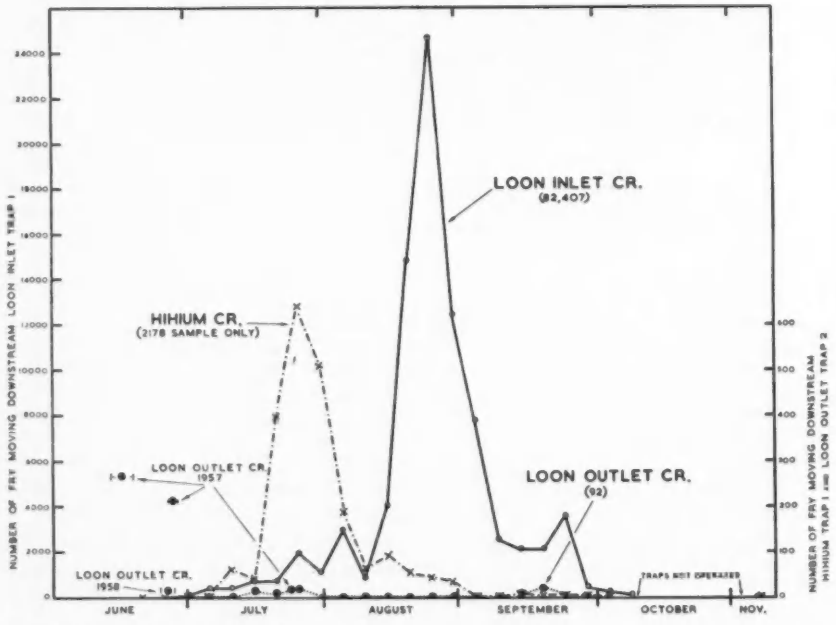

FIG. 4. Seasonal periodicity of downstream movement of rainbow trout fry in streams of the Loon Lake system. Numbers in brackets indicate total number of fry moving downstream in 1953 during period shown.

Downstream movement of fry in Outlet Creek is meagre when compared to that evident in the other two streams. However, free-swimming fry are present in Outlet Creek by early June each year, the 1953 season being no exception. Outlet Trap 2 was not operating that year until June 29 so down-

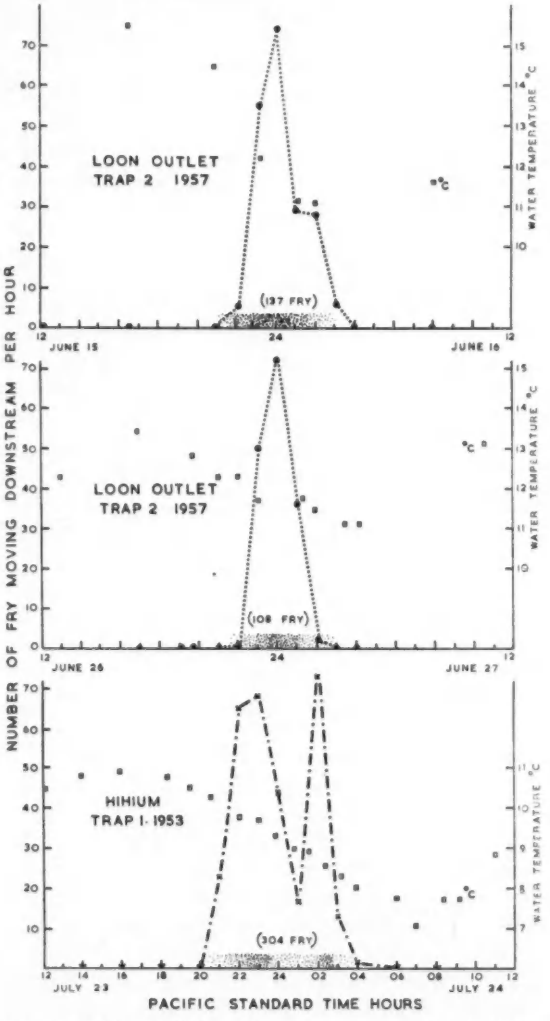

FIG. 5. Diel periodicity of downstream movement of rainbow trout fry in Outlet and Hihium Creeks. Numbers in brackets indicate total numbers of fry moving downstream during period shown. Night hours shaded to indicate degree of darkness (based on field notes).

stream movement of fry prior to that date may have been missed. High discharge of Outlet Creek in June and July 1954 prevented operation of traps with screen fine enough to retain all fry. To examine fry movement in June further, Outlet Trap 2 was operated effectively with fine screen for short periods (2–5 consecutive days) in 1957 and 1958 (Fig. 4). Many fry moved downstream into Outlet Trap 2 in mid and late June 1957, while few were taken during a similar period in late June 1958. No obvious difference in abundance of recently emerged fry was evident between the two years.

In both Inlet and Hihium Creeks there occurs each summer an extended period within which many young trout fry move downstream. Such movement also occurs, at least during some years, at Outlet Creek, but there it is apparently restricted to a few weeks in June even though recently emerged fry are usually present until early August.

2. Diel periodicity

Repeated observation on the 3 streams studied has shown that fry which move downstream do so almost exclusively at night. Results from trap operation over typical periods of approximately 24 hours clearly demonstrate the sharply delineated nocturnal downstream movement of fry (Fig. 5, 6).

At each stream the period of maximum downstream movement usually occurred between 2300 (11 p.m.) and 0100 hours, generally the period of lowest nocturnal illumination. Timing of maximum periods of downstream movement and changes in number of descending fry was not *directly* related to stream discharge or temperature but instead followed changes in nocturnal illumination. Virtually no fluctuation in water level was recorded during many of the observation periods. A gradual decline in water temperature occurred each night while downstream movement of fry began, reached peak intensity and ceased.

Where a more or less regular cycle in nocturnal illumination occurred between dusk and dawn, the concomitant pattern of downstream fry movement followed a sharply peaked form, without marked skewness. Such patterns of nocturnal illumination and fry movement were evident early in the season when nights were short.

Irregular patterns of nocturnal illumination were reflected in the periodicity of downstream fry movement. Early on the morning of July 24, 1953, a short interval of bright moonlight produced a sharp but temporary drop in numbers of fry moving down Hihium Creek (Fig. 5). On the other hand, a heavy fog blanket which obscured the moon early on August 12, 1954, at Inlet Creek resulted in a large increase in descending fry until dawn (Fig. 6).

Larger numbers of fry tended to move downstream on foggy or overcast nights than on bright moonlight nights (cf. August 11–12, 1954 with August 12–13, 1954, Fig. 6). Where nocturnal light conditions were similar, such as at Inlet Traps 1 and 2 (August 3–4, 1953, Fig. 6), the patterns of downstream fry movement also were similar.

Appreciable changes occurred throughout the season in initiation and cessation of downstream movement of fry each night. In June few fry began to move downstream until 2300 hours, and the majority had ceased movement

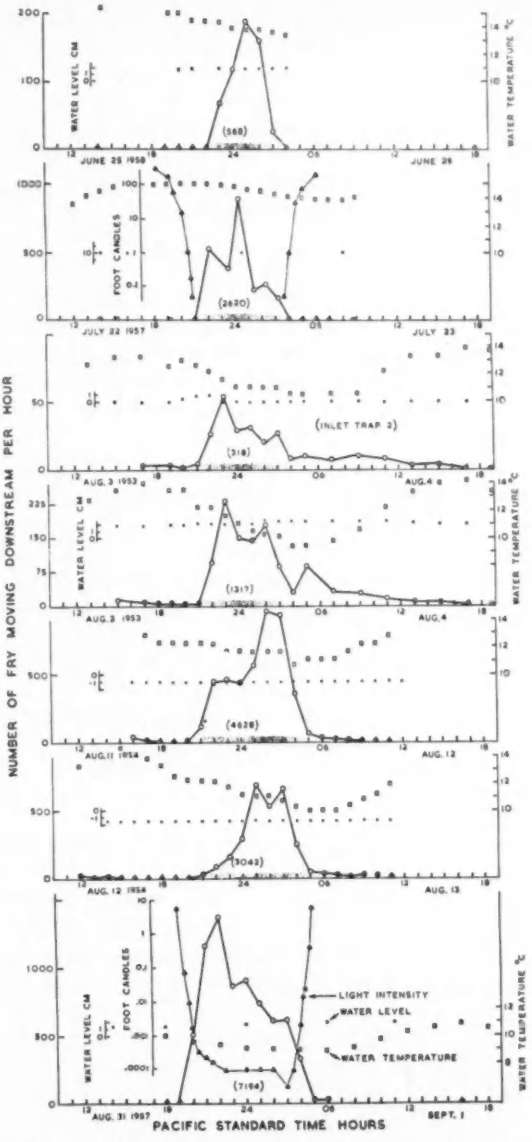

FIG. 6. Diel periodicity of downstream movement of rainbow trout fry in Inlet Creek. Numbers in brackets indicate total numbers of fry moving downstream during period shown. Night hours shaded to indicate degree of darkness (based on field notes). Data from Inlet Trap 1 except where shown otherwise.

by 0300 hours the following morning. By early to mid August considerable numbers of fry began moving downstream by 2200 hours and continued to do so until at least 0400 hours next morning. At the end of August downstream movement began before 2000 hours and did not cease until after 0400 hours the following day. Such seasonal changes in diel periodicity of downstream fry movement are probably related to increase in the length of night throughout summer. A similar relation between nocturnal duration of downstream movement in streams and seasonal changes in day length has been found for sockeye fry (McDonald, 1960).

A more precise examination of the relation between levels of nocturnal illumination and downstream movement of fry was possible for Inlet Creek in 1957 and 1958. Downstream movement of fry began when light intensity fell below 0.01 foot-candle and ceased when it rose above that level with the approach of dawn (Fig. 6, 7). Changes in nocturnal illumination within the range 0.0001 to 0.001 foot-candle are apparently expressed in amount of downstream fry movement.

A separate measure of diel periodicity in downstream fry movement, unaffected by traps, was afforded by counts of fry moving downstream over standard strips placed on the stream bottom (Fig. 7C, D). Thin strips of wood or aluminum, 5 × 30 cm, were firmly anchored onto the stream bottom. Observations and counts of fry passing over such strips were made with binoculars until light conditions required use of infra-red viewing apparatus. All counts were made for 5-minute intervals.

Initiation, rise to maximum, and partial decline in numbers of fry moving downstream over strips on the night of August 30, 1958 (Fig. 7C) agree closely with observations on fry movement into a trap (Fig. 7B) during the same evening. Downstream movement of fry across strips began when light intensity fell below 0.01 foot-candle.

3. Size relationships

Length-frequency distributions of fry moving downstream in Inlet, Outlet and Hihium Creeks are given in Fig. 8. The majority of fry ranged between 20 and 30 mm in length. Information obtained from redd samples of alevins and lengths of free-swimming fry still retaining vestiges of the yolk sac indicated that the free-swimming stage was not reached until the young attained a length of at least 20 mm. Thus most fry involved in downstream movement were recent emergents.

Seasonal changes in length-frequency distribution are evident in fry moving downstream at Inlet Creek (Fig. 8). Although fry of 20–30 mm still predominate among those moving downstream in mid-August to early September, many larger fry also where taken. After early September, at the close of fry emergence, a gradual shift took place in length-frequency distribution of fry moving downstream. By the third week in September the modal group had exceeded 35 mm.

The length distribution of fry moving downstream over a 24-hour period was determined from samples collected at frequent intervals at Inlet Traps 1 and 2 during August 3–4, 1953. Respective length-frequency distributions

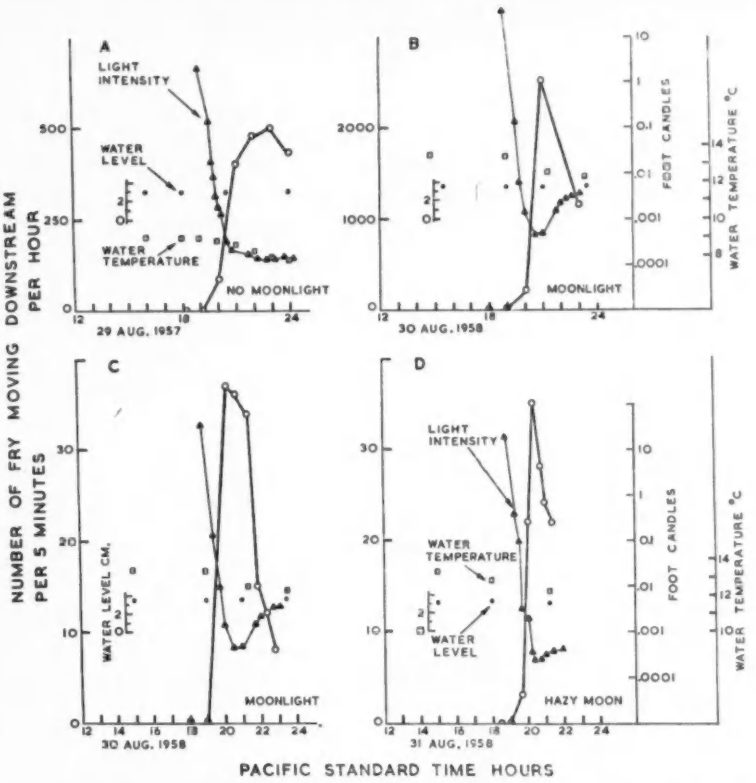

FIG. 7. Initiation of downstream movement of rainbow trout fry in Inlet Creek. **A, B:** downstream fry movement into Inlet Trap 1. **C, D:** downstream fry movement as indicated by counts (infra-red viewing) of fry passing over standard counting strips on stream bottom.

of descending fry were similar for both traps. The few fry which moved downstream during daylight hours were largely in the 30–45 mm length range. With the onset of darkness, considerable numbers of fry between 20 and 30 mm long began moving downstream. The contribution from the 20–25 mm size group was far greater than that from larger groups; in fact numbers of larger fry (30–45 mm) moving downstream in hours of darkness were not greatly different from numbers in this size group which descended in daylight.

4. Extent of movement

Information on distance that fry moved downstream each night was obtained from marking experiments in 1957 and 1958. Six hundred fry were removed from Inlet Trap 1 on the morning of August 31, 1957; all these fish had moved downstream into the trap on the night of August 30. Fry were marked by

"squaring-off" with fin clippers a small portion of the upper, lower or both lobes of the caudal fin. A weak urethane solution was used for anaesthetizing fry. Three lots of 200 fry were marked distinctively and held in screen containers in the stream to recover for one hour. Fry were all swimming actively at the end of an hour and did not show any difficulties in maintaining position in the stream immediately following release. Lots of 200 marked fry were released in small backeddies along the bank 75, 150 and 300 feet (23, 46 and 91 m)

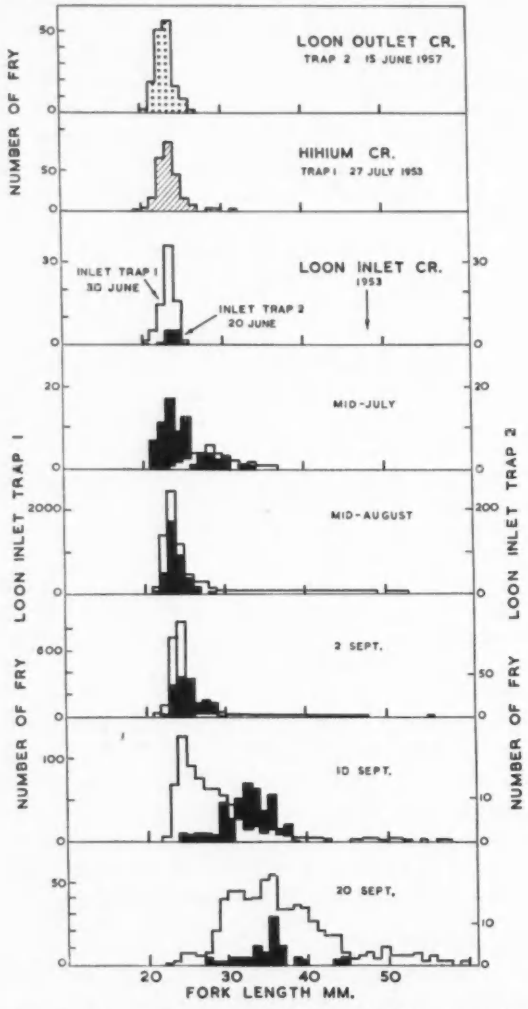

FIG. 8. Length-frequency distribution of rainbow trout fry moving downstream in Inlet, Outlet and Hihium Creeks. *Open bars*, Inlet Trap 1; *solid bars*, Inlet Trap 2.

upstream from Inlet Trap 1 at 1030 hours, August 31, 1957. A similar marking experiment was conducted on the morning of August 30, 1958 releasing two lots of 210 fry 100 and 1000 feet (30 and 305 m) upstream from Inlet Trap 1.

In both years no marked fry were recovered at the trap until after dusk. Many of the fry placed a short distance (75–300 feet, 23–91 m) above the trap moved downstream into it shortly after downstream movement began the first evening after release (Fig. 9A). By next dawn, when downstream fry movement ceased, between 65% and 89% of fry in lots placed up to 300 feet (91 m) above the

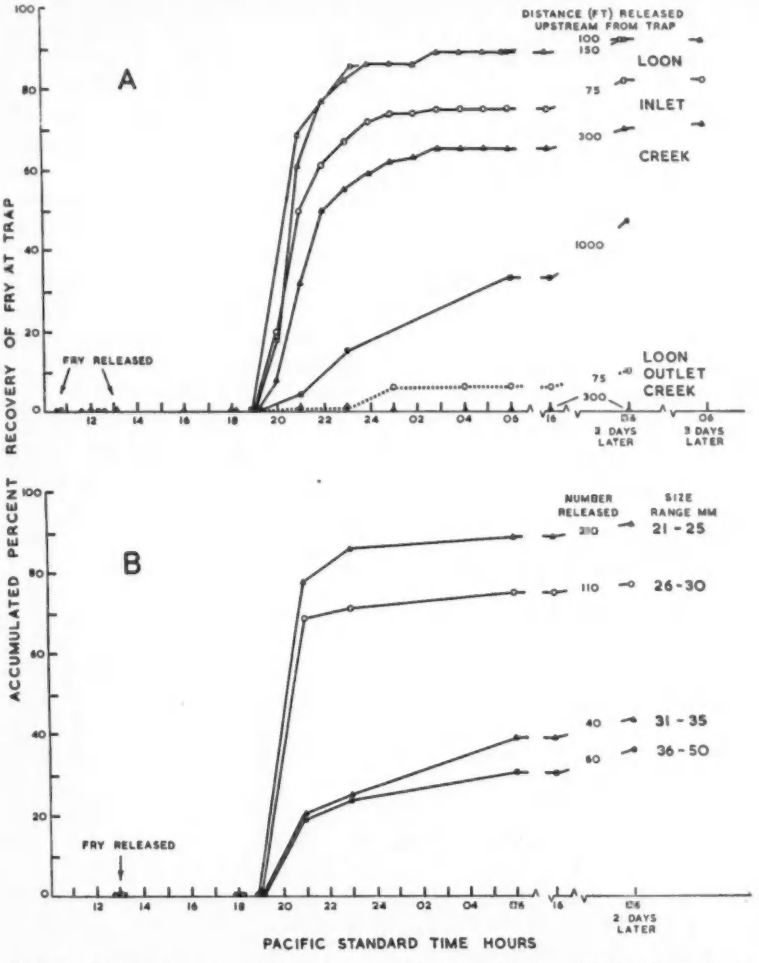

FIG. 9. Extent of movement of rainbow trout fry down Inlet and Outlet Creeks based on marking and recovery experiments. **A.** Recovery of marked fry following release at different distances upstream from traps. **B.** Recovery of different length groups of fry following release 100 feet upstream from Inlet Trap 1.

trap had been recovered. A few fry from these lots were recovered amongst fry moving downstream on the second and third night following release. Only a small number of marked fry placed 1000 feet (305 m) above Inlet Trap 1 were recovered there during the first 2 hours of overnight downstream movement. Less than a third of the fry in this group had been recovered by dawn, although recovery rose to nearly 50% by completion of downstream movement on the second night following release. Many fry apparently moved at least several hundred feet downstream each night. Predation by larger fry and fingerlings upon marked fry may have accounted, in part, for their reduced recovery when placed 1000 feet upstream from the trap.

Results from similar but less extensive experiments with marked outlet fry also are shown in Fig. 9A. Two groups of 106 and 46 marked fry were placed 75 and 300 feet respectively upstream from Outlet Trap 2 at mid-day on June 26, 1957. Only a few of the fry introduced 75 feet upstream and none of those from 300 feet upstream were recovered after two successive nights of trap operation. Fry in the outlet stream in June experienced a much shorter period of darkness than did fry in the inlet stream at the end of August and thus may have moved a correspondingly shorter distance downstream.

A field experiment was conducted to assess the effect of fry size upon extent of downstream movement in Inlet Creek. On the morning of August 30, 1958, a total of 420 fry were measured, marked and released 100 feet upstream from Inlet Trap 1 in a manner similar to that described above. All fry were marked by clipping a small portion off the upper lobe of the caudal fin.

Most fry in the smallest size group had moved downstream within 3 hours after such movement began (Fig. 9B). Fewer intermediate-size fry (26–30 mm) were recovered, while only about 25% of the larger fry were taken within the same period. At the end of the second night similar differences in extent of downstream movement were maintained between small, intermediate, and large fry.

5. Orientation

As almost all downstream movement of fry occurred at night, observation of various features of fry behaviour at that time were made with infra-red viewing apparatus. Orientation of fry in relation to direction of water flow was noted as fry approached 5 × 30-cm strips of aluminum attached to the stream bottom. Fry were counted as "heading downstream" if they approached the strip head first, even though the angle of approach might be acute, and as "slipping downstream" if they approached tail first either at right angles or from a relatively acute angle. Orientation counts were made for 5-minute intervals.

Orientation of fry moving down Outlet Creek was observed on 3 successive nights in June, 1957 for a total of 95 minutes. Of 29 fry observed crossing the aluminum strip during that time, 27 were "heading downstream" more or less in the direction of stream flow. At Inlet Creek 8 counting periods were recorded on the night of August 30, 1958 and 7 on the following night. Out of 308 fry observed during these periods, 219 or about 71% were "heading downstream".

As fry heading downstream approached stones or sticks protruding from the stream bottom, they usually turned sharply and oriented actively into the current for a few seconds. This orientation often took place before the fry came into direct contact with the object. Fry rarely maintained position upon orientation when an object was encountered mid-stream, but merely drifted for a short time with head upstream, then turned and headed on downstream. If this orientation occurred near or at the stream edge, fry occasionally held position there for several minutes. Fry displayed erratic spurts of swimming in a zig-zag fashion as they headed downstream (Fig. 17). Many were at or near the surface of the stream, as shown by their white appearance under infra-red illumination and by the frequent presence of "bow-wakes" from the dorsal fin.

B. Factors Affecting Downstream Movement

1. Water temperature

(*a*) *Relationships in field.* That fry move downstream in Inlet and Hihium Creeks over an extended period during the summer but do not do so in Outlet Creek, represents one of the key problems in understanding migratory behaviour of young trout in the Loon Lake stream system. One of the most striking environmental differences between Outlet Creek on one hand, and Inlet and Hihium Creeks on the other is found in their temperature characteristics.

During July, August and part of September when young free-swimming fry are present in all streams, water temperatures at both Inlet and Hihium Creeks are considerably lower than those prevalent in Outlet Creek (Fig. 2). Maximum daily temperatures of Inlet and Hihium Creeks rarely exceed 15°, while at Outlet Creek even daily minimum water temperatures are usually above 15°. Therefore during that portion of the summer when marked differences were noted in migratory behaviour of young fry between the streams, there was in fact a consistent difference in range of water temperature between these streams. Downstream movement of fry occurred in the two cooler streams.

Nevertheless fry, at least in some years, exhibit downstream movement in Outlet Creek during a few weeks in June. Maximum water temperatures of Outlet Creek during periods when appreciable downstream movement was observed (June 13–17 and June 26–28, 1957) ranged between 10.6 and 16.0°; thus they were usually within the temperature range at which downstream movement of fry was known to occur in Inlet and Hihium Creeks. In 1958 at the time when Outlet Trap 2 was operated for 2 consecutive days and nights (June 24–26) relatively few fry were moving downstream (Fig. 4). Water temperature of the outlet stream at that time was much higher than in the comparable period in 1957, ranging from 20.6 to 24.4°. Thus the occurrence or absence of downstream movement of fry in Outlet Creek also may be related to characteristics of its water temperature.

(*b*) *Fry transfer experiments.* The effect of reciprocal transfer of fry between Inlet and Outlet Creeks was studied by experiments conducted in

TABLE III. Rainbow trout fry transfer experiments in Inlet and Outlet Creeks, 1957 and 1958.

Particulars	Inlet to Outlet	Outlet to Inlet
Date of transfer	2 September 1957	25 June 1958
Time of transfer	0900–0930	1100–1130
Place of transfer	Inlet Trap 1 descending fry placed 75 feet upstream from Outlet Trap 2	Fry collected near Outlet Trap 2 placed 75 feet upstream from Inlet Trap 1
Number of fry transferred	200	174
Size range, mm	21–30	21–30
Temperature of original[a] stream		
Day before transfer	7.7–10.3°	21.1–24.0°
Day of transfer	8.9–10.7°	20.7–22.1°
Temperature range of new[a] stream		
Day of transfer	15.6–18.7°	13.3–15.5°
Day after transfer	15.6–18.8°	12.8–15.0°
Fry moving downstream after transfer		
0–24 hours after	1	9
24–48 hours after	0	14
Fry moving downstream in original stream 0–24 hours before transfer	7194 (Inlet Trap 1)	8 (Outlet Trap 2)

[a]"Original" stream refers to the stream from which fry were taken; "new" stream refers to the stream to which fry were transferred.

1957 and 1958 (Table III). All fry involved in the transfer had moved down Inlet Creek into Inlet Trap 1 during the night before and early morning of the transfer day, along with additional fry that were not transferred. Fry were anaesthetized (weak urethane solution) and marked by clipping a small portion off one lobe of the caudal fin. Following recovery they were moved in covered fry cans to the site of release, 75 feet (23 m) above *Outlet* Trap 2. Here the inlet water in the can was gradually brought up to the temperature of the outlet stream. At this time Outlet Creek averaged nearly 8° warmer than the inlet stream. Fry were introduced into several relatively slow-flowing small pools above Outlet Trap 2 where ready access for movement upstream or downstream was available. Fine-mesh screen across Outlet Trap 2 prevented downstream movement of fry past this point without recovery in its descender trap. Most fry immediately held position at or near the site of introduction. Many were recognized (inlet fry were appreciably smaller than outlet fry at time of transfer) in the same area 26 hours after release and several marked individuals were captured by dip-netting at the introduction site 48 hours after release. Only one of the 200 inlet fry transferred to the outlet moved downstream into Outlet Trap 2 on the night following release, although all had descended into Inlet Trap 1 the night previously (Table III). None were taken on the second night following release.

When the same number of inlet fry had received similar marking, retention, release treatment (except for a slightly shorter period in fry cans) and were placed 75 feet above *Inlet* Trap 1 on August 31, 1957, more than 80% moved downstream within the first 4 hours of that night (Fig. 9A). Apparently a

marked alteration in current response of the inlet fry had occurred subsequent to their release in the outlet stream. The most striking difference between the two streams at the time of transfer was in temperature.

Reciprocal transfer of similar size groups of fry from outlet to inlet could not be made in late summer of 1957 because no small outlet fry were available then, but this was done early the next summer (Table III). As very few outlet fry were moving downstream into outlet traps in June, 1958, individuals for the experiment were collected during the day by dip-netting. Marking and transfer methods were similar to 1957 experiments. Of the 174 outlet fry placed above Inlet Trap 1, 9 were recovered there early on the first morning following transfer and 14 others were taken after the second morning. Although large numbers of outlet fry did not move downstream in the first two days after transfer to the inlet, nevertheless this movement was appreciably higher than in the reverse transfer, and much higher, proportionately, than that taking place in the outlet stream where thousands of fry above Outlet Trap 2 were available to move downstream. Transfer of outlet stream fry into the colder waters of Loon inlet Creek resulted in much more downstream movement than was characteristic of these fry in warmer water of the outlet stream.

(c) *Experimental flume studies.* A convenient field set-up was available at the confluence of Outlet Creek and Hihium Creek to study the effect of their waters, which differed markedly in temperature, on downstream movement of trout fry in two experimental flumes placed side by side.

Rainbow trout fry were introduced into the centre section of each flume in the early morning and left undisturbed throughout the day. At dusk the fry in each compartment of the flumes and in the Wolf traps below were counted and returned to the centre compartment where they were left until early the following morning. At that time fry again were counted and returned to the centre compartment. This procedure was continued for several days on one lot of fry. Approximately 50 fry were used in each flume.

Most experiments were carried out with 1954 Outlet fry which had been reared at Loon Creek Hatchery (spring water) where summer water temperatures did not vary appreciably from 9°. One experiment utilized fry collected from Inlet Creek (Inlet Trap 1). The outlet fry ranged between 23 and 28 mm in length while those from the inlet were slightly smaller.

Movement was expressed as the number of compartments fish had moved downstream or upstream from the centre compartment. A summed score was thereby obtained for movement in either direction over the interval that fry were left undisturbed (Fig. 10).

In 9 out of the 10 consecutive experiments, more downstream movement was shown by fry in the flume supplied with Hihium Creek water, when compared with that in the flume with Outlet Creek water during the same period. In the one experiment utilizing fry from Inlet Creek results were similar to the remainder of experiments with fry from Outlet Creek.

On August 8, 1954, fry which had been held in the flume with Outlet Creek water since the evening of August 3 were transferred to the flume supplied with

Hihium Creek water and fry from the latter flume were moved to the flume with Outlet water. All fry were placed in the centre compartment, as in previous experiments, and were not counted until early the following morning. Their current response during the interval was consistent with that for the new flume (Fig. 10).

Between August 10 and 11, 1954, fry distribution in the flumes, following the same methods of introduction as used previously, was checked every 3 hours from early morning to dusk (when fry were again returned to the centre compartments) and then periodically throughout the night. Numbers of fry moving downstream into the Wolf traps at the end of each flume increased gradually throughout the day and night.

2. Light

The effect of alternate periods of lantern light and darkness on periodicity of downstream movement of fry was tested at Hihium Creek (Hihium Trap 1)

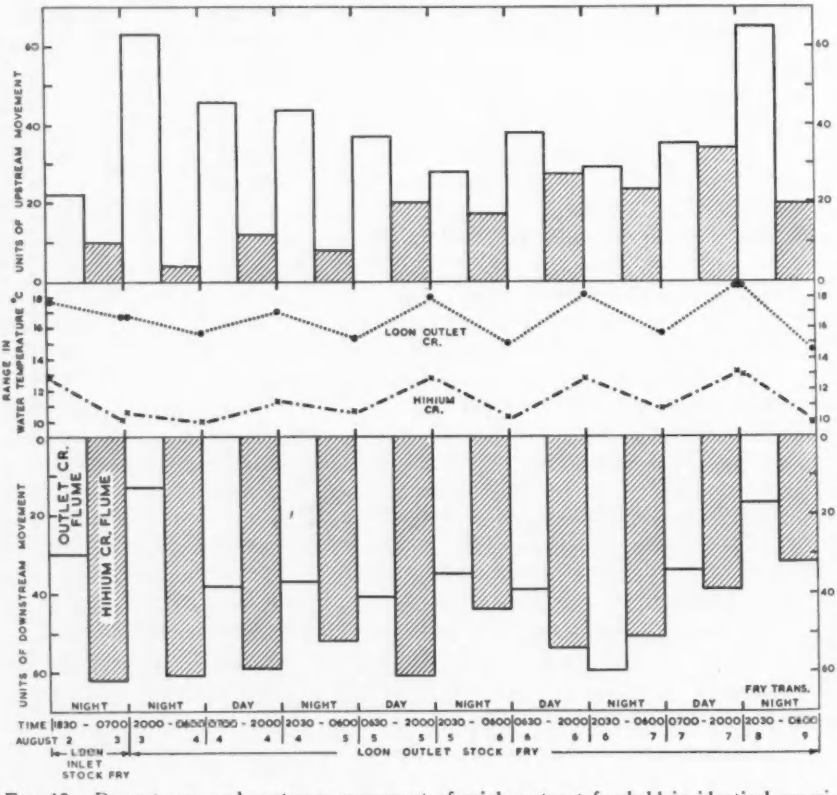
UNITS OF UPSTREAM MOVEMENT
RANGE IN WATER TEMPERATURE °C
LOON OUTLET CR.
HIHIUM CR.
UNITS OF DOWNSTREAM MOVEMENT
OUTLET CR. FLUME
HIHIUM CR. FLUME
NIGHT
DAY
FRY TRANS.
TIME 1830 - 0700 | 2000 - 0630 | 0700 - 2000 | 2030 - 0600 | 0630 - 2000 | 2030 - 0600 | 0630 - 2000 | 2030 - 0600 | 0630 - 2000 | 2030 - 0600 | 0700 - 2000 | 2030 - 0600
AUGUST 2 3 3 4 4 4 4 5 5 5 5 6 6 6 6 7 7 7 8 9
LOON INLET STOCK FRY
LOON OUTLET STOCK FRY

FIG. 10. Downstream and upstream movement of rainbow trout fry held in identical experimental flumes, one supplied with Outlet Creek water, the other with Hihium Creek water, August 2–9, 1954.

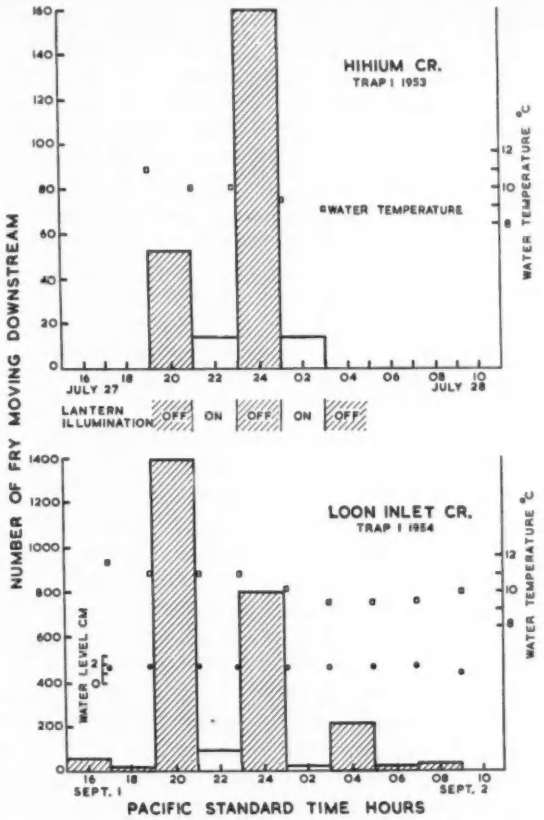

FIG. 11. Effect of alternate periods with and without lantern illumination on downstream movement of fry in Inlet and Hihium Creeks.

and Inlet Creek (Inlet Trap 1). In each experiment a 300 candle-power Coleman gasoline lantern was suspended over the stream a few feet upstream from the trap and turned off and on at 2-hour intervals during the night. Fry were removed from the trap and counted at the end of each 2-hour period. At both streams, fewer fry moved downstream during intervals with lantern illumination than during previous periods without such illumination (Fig. 11). No marked changes in natural nocturnal illumination, except those associated with setting and rising of the sun and moon, occurred during either experiment.

3. COMBINED EFFECTS OF WATER TEMPERATURE AND LIGHT

Laboratory studies on downstream movement of rainbow trout fry at different temperatures and under several levels of illumination were conducted in the experimental stream in 1955, 1957 and 1958.

In one group of experiments a 7.3-metre length of stream was utilized; the rest of the stream containing pumping and temperature control apparatus was blocked by perforated aluminum screens at each end. The bottom of the portion utilized was marked off into 13 sections of approximately the same length by 5-cm-high baffles placed against the bottom at right angles to the direction of flow. At a total depth of 10 cm of water in the stream, used for all experiments in this series, water velocity over each baffle averaged about 6 cm/sec.

Eggs collected from the *Outlet* spawning run in May 1955 were reared at Loon Creek Hatchery at about 9° until eyed, when they were transported to the laboratory. Hatchery water temperature there varied between 9 and 11.5° throughout the course of experiments. On July 16, 1955 about 100 fry from this stock were transferred to an aquarium maintained at 15° (±0.5°); another group of about the same number was changed to 18° (±0.5°) on July 26. Fry were 21 to 26 mm in fork length.

Thirty fry were transferred from holding troughs or aquaria into the middle section of the experimental stream maintained at the same temperature and surface light intensity as fry experienced in the holding facilities. Fry were free to move upstream or downstream into any one of six sections in each direction. After a 2-hour period following introduction the distribution of fry was noted and light intensity reduced over a 15-minute interval to the next lower level tested. Distribution of fry was noted after each period of reduction. A shielded pen-light with a red filter was used to make counts at the two lowest light intensities. A method similar to that used in field flume experiments was employed for expression of upstream and downstream movement. The number of fry counted in each successive section away from the middle section was multiplied by a factor increasing by 1. Units of upstream and downstream movement were summed for each observation period.

Results of all the above experiments are shown in Fig. 12 (upper). Marked differences are evident in amount of downstream movement shown by Outlet fry held at different temperatures. Those held in hatchery water at about 10° exhibited much more downstream movement, particularly at lower light intensities, than did those held over a week at temperatures 5 or 8° higher.

In another series of experiments similar groups of fry were introduced to the middle section of the stream as before. This section was provided with a gravel bottom. Perforated aluminum screen barriers, resting on the baffles at the upper and lower ends of the middle section prevented exit of fry. Light intensity was gradually reduced for 15 minutes, then the lamps were turned off. Barriers at the ends of the middle section were then removed, leaving fry free access for upstream or downstream movement as in the previous series of experiments. Counts were made of fry distribution in sections of the experimental stream after they had remained 15, 30, 45, 60, and 75 minutes in darkness. Results of the 7 experiments are given in Fig. 12 (middle). As in the previous experiments, fry from Outlet Creek held at low temperature (about 10°) showed appreciably more downstream movement in the experimental stream than did similar fry held 14 to 20 days days 16 and 18°.

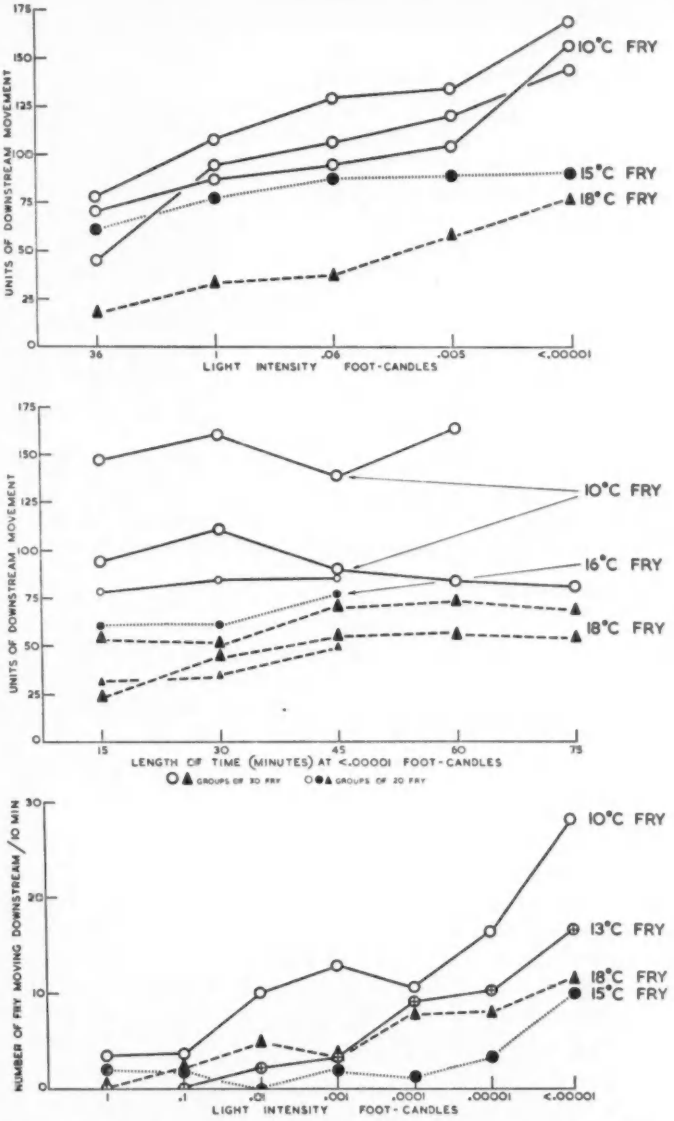

FIG. 12. Downstream movement exhibited by rainbow trout fry in experimental stream at different temperatures and conditions of illumination.

Upper: Outlet stock.

Middle: Outlet stock held in stream at low light intensity (<0.00001 foot-candle).

Lower: Loon Inlet stock (13 and 18° fry) and Pennask Lake Inlet stock (10 and 15° fry).

In another series of experiments in the experimental stream, the partitions at each end of the temperature control section (Fig. 3B) were removed, permitting fry to move continuously either upstream or downstream. A perforated aluminum shield was placed in front of pump intakes to prevent fry from entering the pumps. At the water depth of 15 cm used in this series the maximum velocity was about 10 cm/sec (mean cross-sectional velocity 4.2 cm/sec). Twenty fry were introduced into the same section of the stream as in previous experiments and observations started 30 minutes after introduction. Numbers of fry passing upstream and downstream over a 5-cm-wide strip placed across the flume in the centre of the introduction section were counted for 10-minute intervals. Counts at low levels of illumination were made with infra-red viewing apparatus. Fry used were 22 to 26 mm long. Reduction to the next lower level of illumination was made gradually (over 5 minutes) by means of an iris diaphragm in a lamp housing. Indirect illumination was provided by reflecting light from the lamp housing off the ceiling of the room containing the experimental stream.

Results of this series of experiments on *Inlet* stock from Loon Lake and Pennask Lake are presented in Fig. 12 (lower). Particularly at low levels of illumination, downstream movement was more pronounced in the groups of fry held at 10 and 13° than in those held for over 14 days at 15 or 18°.

4. Size of fry

Observations in the field suggested that downstream movement of fry in Outlet Creek involved a higher proportion of small fry than would be expected on the basis of the length-frequency distribution of those holding position in the stream during the day. Furthermore, marking and recapture experiments (Fig. 9B) at Inlet Creek suggested that small fry (21–30 mm) exhibited more downstream movement than did large fry (31–50 mm). Both observations indicate that size may be of importance in affecting downstream movement of fry.

Throughout autumn and winter, fry in Outlet Creek exhibit virtually no downstream movement even though water temperatures at that time drop well within the range at which downstream movement occurs at Inlet and Hihium Creeks. Nearly all fry in samples of young trout collected by seining in Outlet Creek at the end of August exceeded 40 mm in length. Apparently downstream movement of these larger fry, even in declining water temperatures, is not appreciable at Outlet Creek. At Inlet Creek, however, some downstream movement of fry larger than 40 mm did occur in September (Fig. 8).

DOWNSTREAM MOVEMENT OF FINGERLINGS

A. Characteristics of Downstream Movement

1. Seasonal periodicity

Movement of fingerlings down streams of the Loon Lake system is shown in Fig. 13. The total given for Hihium Creek probably represents somewhat

more than 25% of the total number moving downstream, as the trap there usually did not screen the whole creek volume.

Few fingerlings moved downstream at Outlet Trap 2 while virtually none were recorded as descending into Outlet Trap 1. At Outlet Trap 4, which sampled between 1/10 and 1/3 of the stream depending on discharge, only 18 fingerlings moved downstream during its continuous operation from May 20 to October 14, 1953. Only 1 descending fingerling was taken at this trap during a sampling period from November 4–8, 1953, and only 15 between March 18 and May 14, 1954. Permanent loss of fingerling trout from the Loon Lake system by passing over the falls is apparently negligible. Considerably more fingerlings moved downstream in Hihium Creek and Inlet Creek than did in Outlet Creek. In all streams the majority of downstream movement of fingerlings occurred in late spring and early summer.

2. Diel periodicity

No marked diel periodicity (such as shown by fry) in downstream movement was evident for fingerlings in any of the streams studied. During most of the periods over which traps were checked at short intervals for 24 hours or longer, more fingerlings moved downstream at night than during daylight hours.

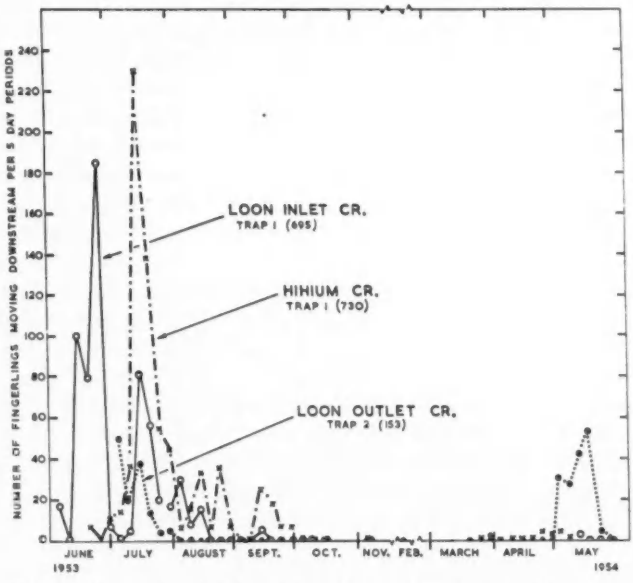

Fig. 13. Seasonal periodicity of downstream movement of rainbow trout fingerlings in streams of the Loon Lake system. Numbers in brackets indicate total number of fingerlings moving downstream during period shown.

B. Factors Affecting Downstream Movement

Field evidence (Fig. 13) suggested that downstream movement of fingerling trout was predominant in streams of the Loon Lake system having cool summer water temperatures, i.e. Inlet Creek and Hihium Creek. Most of this movement occurred at a time of the year associated with long days and short nights, but the marked diel periodicity of downstream movement typical for fry was not so pronounced among fingerlings.

Response to water current of fingerling rainbow trout (hatchery stock) held at different temperatures and day lengths was tested in the experimental stream at the laboratory. Rainbow trout fingerlings were held in 6 tanks during October, 1957. Two tanks were kept at 10°, two at 15° and two at 20° (control ±0.5°). On November 4, 1957, light hoods were placed on each tank. One set of tanks at 10, 15 and 20° received 8 hours' illumination alternating with 16 hours' darkness, while 3 others at the same temperatures received 16 hours' illumination alternating with 8 hours' darkness. Incandescent bulbs (7.5 watt) provided illumination varying between 2.4 and 4.8 foot-candles at the water surface during the "day" period.

Fish tested in the experimental stream were free to swim in either direction around the apparatus without interruption, and when doing so were said to "cycle" with or against water current. Illumination from an overhead incandescent lamp varied between 0.5 foot-candle in shade of the stream wall and 7.5 foot-candles in direct light at the water surface. At a water depth of 15 cm a current with a maximum velocity of 9.7 cm/sec (mean cross-sectional velocity of 4.2 cm/sec) was maintained in the experimental stream. Cover and resting positions were provided for fish by placing stones (15 to 25 cm diameter) at intervals along both sides of the stream.

Fish were removed from a holding tank, placed in the stream at their previous temperature (maintained throughout the test) and left for one hour before observation. All observations were made during "day" periods for fish tested.

Groups of 5 fish were used for each experiment. Reactions to current were measured by counting the number of times fish made a complete cycle around the stream, either upstream or downstream within a 5-minute period. Number of cycles around the stream made by all fish in the group within a 5-minute period was taken as a unit measurement of movement. Observations were continued at intervals until responses were recorded for from 9 to 15 separate 5-minute periods. Replications (3 to 5) were made with different lots of 5 fish at each temperature and day length. Experiments were started 41 days after fish were first exposed to controlled day length and were completed 40 days later.

Fingerling trout used in experiments ranged between 55 and 125 mm in fork length. No difference was noted in gonadal development between 8-and 16-hour fish either in gonad appearance or in a gonad to total body weight comparison. Gonads appeared to be characteristically immature.

Fingerlings held at 10° and long day length showed a greater tendency to move downstream than did those held at the same day length but at 20° (Fig. 14). These results tend to support the generalizations made from field observations at the Loon Lake stream system where fingerlings at low temperature (Hihium Creek and Inlet Creek) during the long day length period (June and July) moved downstream in much greater numbers than did fingerlings at the same period in warm water of Outlet stream (Fig. 13). In addition, fingerlings under autumn and winter conditions of low temperature and short day length exhibited very little downstream movement in any of the streams studied. Experimental results given in Fig. 14 for fingerlings held at 10° and 8-hour day length again suggest that the particular combination of water temperature and day length may be of considerable importance in regulating migratory patterns. The depressing effect of short day length on downstream movement was expressed at all temperatures tested.

In addition, the effect of temperature change on downstream movement was tested with fingerlings held at different temperatures and day lengths. Only one group of 5 fingerlings which had been held at 8-hour day length was studied at each initial temperature (10, 15, 20°) while 2 groups of 16-hour day length fish were used. Responses of fingerlings to water current were recorded on over 9 separate 5-minute periods with each group of fish at each temperature.

Groups of 5 fingerlings held under the same conditions as in previous experiments were subjected to an increase of 5° in the experimental stream. Fingerlings first were introduced to the stream at their previous holding temperature (holding time at least 3 months) and a series of observations made on their response to current as before. Then a number of immersion heaters were turned on while fingerlings remained in the experimental stream. In less than 2 hours the stream temperature was raised 5° and another series of observations of current response of fingerlings was started. Fingerlings were then transferred to holding tanks maintained at the appropriate day length and new temperature until their response in the stream was again tested 24 and 72 hours after the initial temperature increase.

Increases in temperature produced no appreciable change in the slight amount of downstream movement shown by 8-hour day length fingerlings. In both lots of 10° fish held at 16-hour day length, under which conditions a considerable amount of downstream movement occurred (Fig. 14), downstream movement decreased immediately following the 5° increase. After 24 hours downstream movement had further decreased in one lot and had completely ceased in another.

The immediate effect of a 5° decrease in temperature was examined only in 16-hour day length fingerlings. Experimental procedure was the same as in temperature increase tests except for the 5° decrease which required about 2.5 hours. In the groups of fish held at 10 and 15°, which exhibited considerable downstream movement at their respective holding temperature, downstream movement was reduced immediately following the temperature decrease. Longer term effects of these decreases in temperature were not examined, however results given in Fig. 14 would indicate an eventual increase in downstream movement at lower temperature under long day length.

MAINTENANCE OF POSITION BY FRY

Movement of young trout in streams of the Loon Lake system is undoubtedly essential to their eventual residence in Loon Lake itself. However, maintenance of position is of prime importance to young trout in Outlet Creek if they are to remain within the system before entering the lake. Futhermore, young trout maintain position in Hihium Creek and Inlet Creek at least during daylight hours. An understanding of the migratory behaviour of juvenile trout in the Loon Lake stream system requires consideration of their characteristics and mechanisms of position maintenance in flowing water.

A. Characteristics of Position Maintenance

1. Size and specificity of "holding area".

In the first few weeks following emergence from redds, fry in Outlet, Inlet and Hihium Creeks maintain position, at least during the day, without appreciable movement either upstream or downstream. Continuous observation of small groups of fry within local areas for several hours as well as marking and recapture experiments showed that fry in both Inlet and Outlet Creeks maintain position during the day within restricted areas, often less than 1 foot from where they were initially observed or marked. Groups of young fry at Outlet Creek were recovered over a week later in the same small pool or riffle where they had been marked and released. On the other hand, fry moving

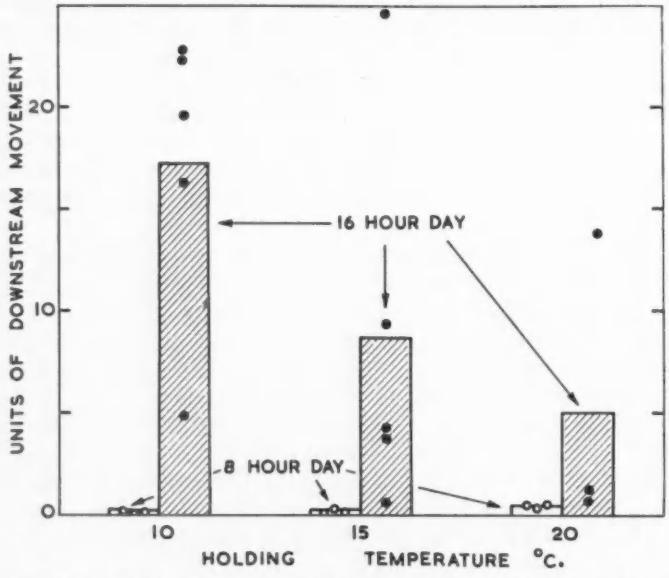

Fig. 14. Downstream movement exhibited in experimental stream by rainbow trout fingerlings held at different combinations of temperature and day length. Dots represent individual lots; columns are averages.

down Inlet and Hihium Creeks at night must occupy new holding areas each day.

2. Change of holding areas between day and night

Observations in both Outlet and Inlet Creeks during the day and at night with infra-red viewing apparatus suggested that fry changed their holding position in the stream between day and night. Quantification of the shift was accomplished by counting numbers of fry holding position within areas marked off by string boundaries (above the water surface) both along and away from the stream margin. During the day counts were made with 7 × 50 binoculars from a vantage point where fry in counting areas would not be disturbed. At Outlet Creek a counting site a short distance upstream from Outlet Trap 2 was chosen, while at Inlet Creek counts were made in areas both above and below Inlet Trap 1. At each counting site a strip along the stream margin

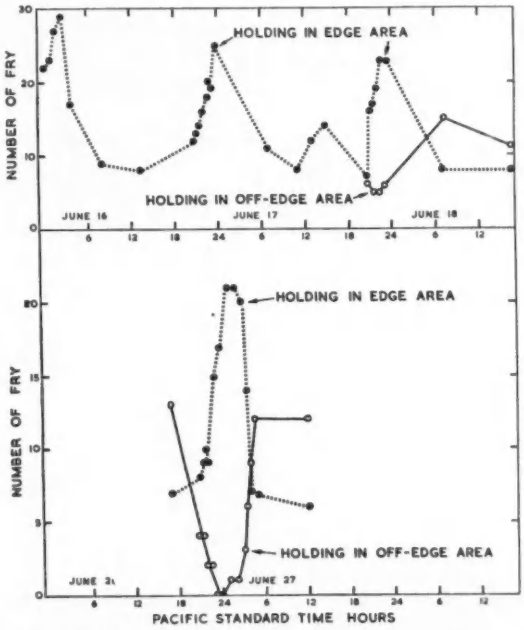

Fig. 15. Diel changes in number of rainbow trout fry maintaining position in edge and off-edge areas of Outlet Creek, 1957.

12 inches wide and 36 inches long (30 × 91 cm) was designated as an "edge" area; an adjacent strip of the same width and length towards the centre of the stream formed the "off-edge" area. Where large numbers of fry were present in counting areas (such as in "edge areas" at Inlet Creek on the night of July 22, 1957) counts were approximate and probably minimal.

Results of fry counts in "edge" and "off-edge" holding areas at Outlet Creek are given in Fig. 15. Those for an area above (July 22–23) and below (August 30 to September 1) Inlet Trap 1 are given in Fig. 16. General features of the shift in holding areas are similar at both streams. During the day few fry held position in edge areas whereas appreciable numbers were dispersed in off-edge areas of the stream. At night the situation was reversed with many fry in edge areas and few fry occupying off-edge areas.

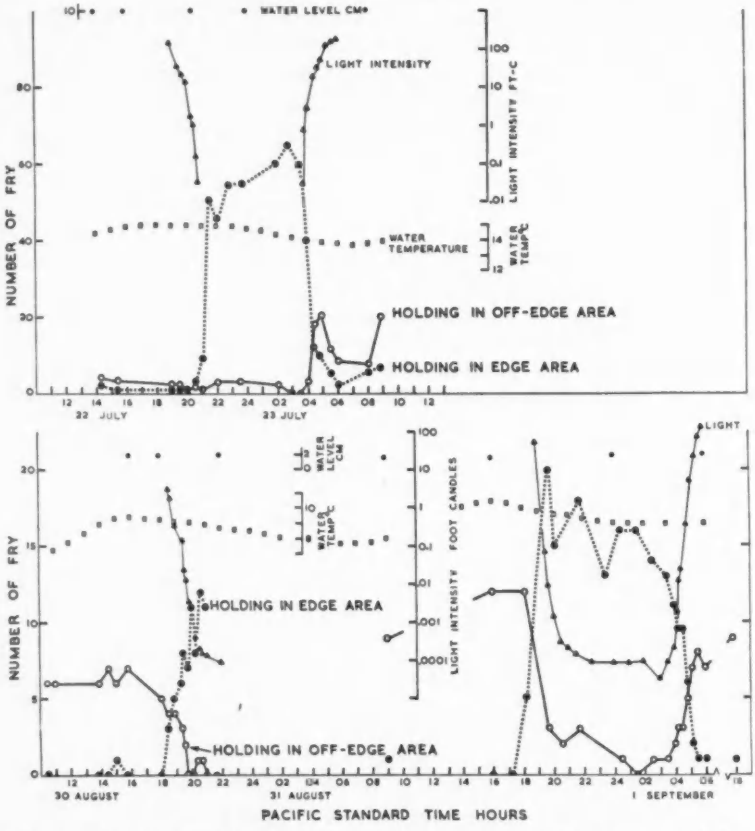

FIG. 16. Diel changes in number of rainbow trout fry maintaining position in edge and off-edge areas of Inlet Creek, 1957.

The marked shift in position of fry laterally in the stream at dusk and dawn each day appeared to be more directly related to changes in illumination rather than in water temperature or level (Fig. 16). This shift usually took place when illumination dropped (at dusk) or rose (at dawn) beyond the range 10 to 0.1 foot-candles. Differences in timing of the shift between June (when

it occurred later in the evening and earlier in the morning) and early September (when it occurred earlier in the evening and later in the morning) also may be related to seasonal changes in the daily cycle of illumination.

Movement of fry from midstream areas towards the stream edge in the evening appeared to be a positive movement rather than a slow, irregular shift in position. Detailed observations on the nature of this movement were made on the evening of August 31, 1957, along a short stretch of stream edge below the counting area downstream from Inlet Trap 1. At 1810 hours a group of 6 fry which had recently moved onto the stream edge from off-edge areas were disturbed by the observer; the fry moved laterally about 2 feet (0.6 m) out towards the stream centre. Within one minute 6 fry had moved back into the edge area and were holding position. Between 1811 and 1820, 6 fry were disturbed from the edge area 3 additional times — on each occasion 6 fry quickly returned to the stream edge, where they held position. Although it could not be deter-

FIG. 17. Diagrammatic representation of disturbance of dense groups of rainbow trout fry maintaining position along margin of Inlet Creek in darkness (based on observations with infra-red viewing apparatus). **A.** Fry swimming erratically downstream near surface approaches group of fry maintaining position at stream margin. **B.** Group of fry rapidly disperses when closely approached or contacted by fry swimming downstream. **C.** Several fry from group move out towards centre of stream, others move closer towards stream margin. **D.** Fry leaving edge turn downstream and begin erratic swimming movement; those at edge orient positively to current and continue to maintain position.

mined positively that the 6 fry which returned each time were the same ones which were there previously, the distinctive marking and size of 2 fry suggested that at least some were the same individuals.

3. Disturbance of fry holding position

Repeated night observation (infra-red) at Inlet Creek showed that sudden intrusion into a dense group of fry near the stream edge by fry moving erratically downstream resulted in violent disturbance of the group. When fry which were erratically heading downstream suddenly turned towards the edge of the stream and "struck headlong" into a dense group of fry along the margin, the reaction of the group was virtually explosive. Most individuals in the group scattered wildly, many heading away from the edge into the middle of the stream, whereupon they themselves headed downstream. The sequence of events leading to and following such disturbance of a fry cluster along Inlet Creek margin is depicted in Fig. 17. Similar disturbances of densely packed groups of fry along the stream edge occurred when one fry in a group attempted to nip another, usually following bodily contact by two individuals holding position close together.

B. Factors Affecting Maintenance of Position

1. Combined effects of temperature and light

A series of laboratory experiments examining effect of water temperature and light on behaviour associated with maintenance of position in water current by trout fry was conducted in the autumn of 1955 and spring of 1956 at Cambridge, England.

Rainbow trout fry used in all experiments were reared from eyed eggs (Nailsworth hatchery stock) in constant-temperature aquaria. Four lots of young were maintained at 5, 10, 15 and 20° for at least 20 days before experiments were started. Fry utilized were between 23 and 27 mm in length. All tests were conducted in the experimental chamber described previously (Fig. 3A).

(a) *Activity.* Groups of 5 fry were transferred from holding trays in constant temperature aquaria to the experimental chamber which was held at the same respective temperature. Water current in the chamber was maintained at about 2.7 cm/sec., Illumination from an incandescent lamp suspended above a ground glass lid covering the chamber was 2.5 foot-candles on the water surface and 1.0 at the bottom of the chamber. This intensity was used for all observations in the light. Light intensity in the dark was less than 0.00001 foot-candle, measured with a photomultiplier described by Jones (1955).

All observations in the light were started in the afternoon and extended until early evening. Illumination was then gradually reduced by means of a "variac" over 15 minutes until the room was in darkness. Observations in the dark, utilizing infra-red viewing apparatus were then commenced. The change from light to dark conditions in the experimental chamber occurred at about the same time of day as fry had experienced previously in the aquaria.

As a measure of activity, counts were made of the number of times within a 15-minute period each of the 5 fry crossed a vertical line dividing the chamber

into anterior and posterior halves. The first period of observation in the light began one hour after fry were introduced into the chamber. Observations were made at least once an hour for 3 to 4 hours before the change was made to darkness for a similar series. Similar observations were made on single fry.

Results are presented in Fig. 18. Averages are based on from 2 to 4 groups of individuals, each observed at hourly intervals for at least 3 hours in light and in the dark.

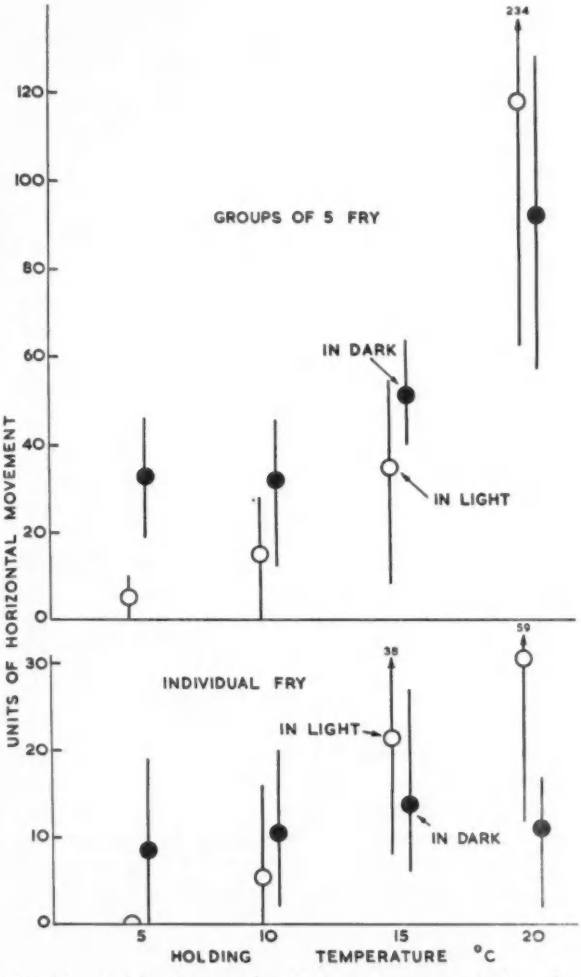

FIG. 18. Activity (expressed as horizontal movement) of rainbow trout fry in experimental chamber at different temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

Activity of fry in the light, when measured in groups or by individuals, increased rapidly at higher temperatures. At 5 and 10° movement of the fry increased in the dark over that shown during the light. However, at 20° activity of fry in the dark usually was less than that in the light, especially in experiments with individual fry. In the latter group, little difference was evident between fry at different temperatures in degree of movement in the dark: those held at 5 and 10° were more active than in the light, while those at 15 and 20° were less so.

These experiments suggest that at higher temperatures fry shift back and forth more while maintaining position in the day but less so at night, a behaviour characteristic which could lead to greater familiarity with the surroundings and thus perhaps greater ability to maintain position when visual contact with the environment is removed or at least greatly reduced. The reverse behaviour, shown by fry held at 5 and 10°, may favour loss of position in flowing water at low levels of illumination.

(*b*) *Depth distribution.* Observations on depth distribution of fry in the experimental chamber were made in conjunction with those on activity. A

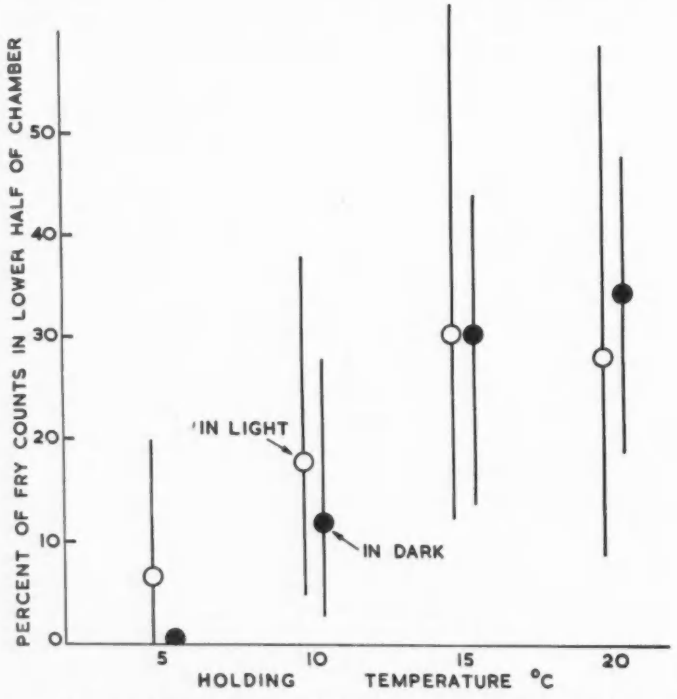

FIG. 19. Depth distribution of rainbow trout fry in experimental chamber at different temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

horizontal line was drawn across the front and back wall of the chamber half way up from the bottom, separating it into upper and lower sections each 7.5 cm in depth. The number of fry (using groups of 5) in each section was counted at 30-second intervals for 15 minutes at a time.

In Fig. 19 each circle represents the average of at least five 15-minute observation periods. At all temperatures, both in light and dark, more fry were recorded in the upper than in the lower half of the chamber. However, at 5 and 10° fry rarely occurred near the bottom, while at 15 and 20° they frequently settled down toward the bottom. At 5 and 10° fry usually remained just under the surface for considerable periods of time, particularly in darkness.

Young fry which, in darkness and in flowing water, spend most of their time at or near the surface would appear much more likely to lose spatial orientation and be carried or move downstream than those that stay close to the bottom. If so, then fry inhabiting warm streams (15–20°) should more readily maintain position at night than those in cool streams (5–10°).

(*c*) *Association with bottom.* A measure of tactile association which fry had with the bottom in flowing water was obtained by counting the number of times they touched or rested briefly on the bottom of the experimental chamber. Fry were introduced into the chamber and held at their previous temperature. A series of observations started 1 hour later in the light followed by another series in the dark, using similar conditions and procedures as described for activity recording. Experiments were made using groups of 5 fry as well as individuals. Counts, for a 15-minute period, were made once an hour during at least 3 hours on each group or individual tested.

Figure 20 shows series of counts for periods totalling 3 hours or longer, from at least 2 different groups or individuals. Fry exhibited little contact with the bottom in the light at all temperatures. Those held at 5, 10 and 15° often swam or maintained position for 15 minutes without touching the bottom of the chamber. In the dark at 15 and 20° fry increased contact with the bottom over that shown in the light. They frequently settled onto the bottom and remained there for brief intervals, rarely for longer periods. Fry at 5 and 10° increased contact with the bottom only slightly in the dark. Experiments with groups and individuals gave similar results.

In addition, a few experiments were performed on the effect of sudden and prolonged temperature change. On one day the contacts made by an individual fry were recorded at its holding temperature (holding time at least 14 days) in the experimental chamber, after which it was returned again to its appropriate constant temperature aquarium. The next day the same fry was placed in the experimental chamber held 5° above or below the previous holding temperature of the fry. After an hour, records of bottom association were made as before over a 3- to 4-hour period, whereupon the fry was placed in a constant temperature aquarium at the new higher or lower temperature. After a period of 7 to 10 days the bottom association of this fry was again recorded at its new temperature. Two experiments were conducted at each holding temperature. Control experiments, where a fry was not subjected to any temperature change,

indicated that individuals maintain a reasonably consistent reaction to the bottom, at least for 10 days.

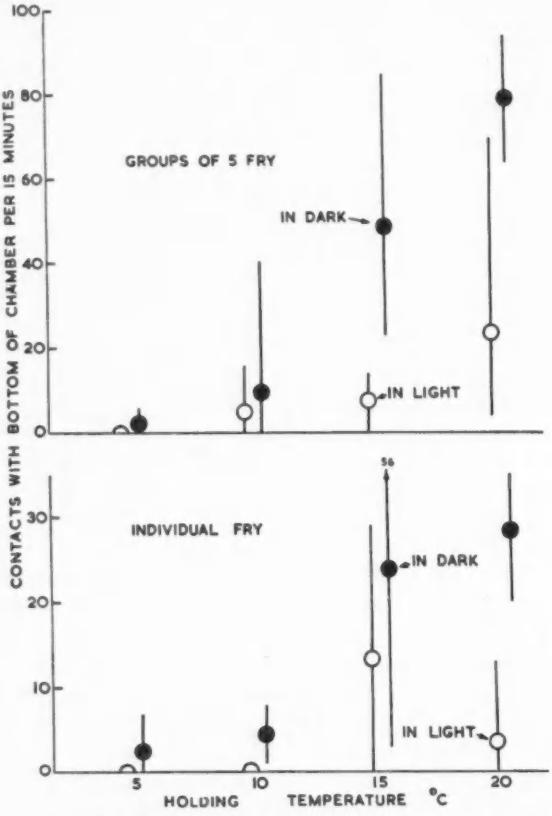

FIG. 20. Association with bottom by rainbow fry in experimental chamber at different temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

Figure 21 gives the reaction *in the dark* of individual fry. Association with the bottom in the light was slight at all temperatures and was not appreciably affected by temperature changes. Where fry experienced an increase of 5° from holding temperature an immediate increase in contact with the bottom was noted. This increase was greater in the change from 10 to 15°, than from 5 to 10°. After 7 to 10 days, bottom contact continued to increase after both changes. Where individual fry were subjected to a decrease of 5° from their holding level, an immediate drop in bottom contact occurred for the 3 changes examined, 20 to 15°, 15 to 10° and 10 to 5°. The decrease appeared to be somewhat greater in the 15 to 10° change than in others. After a period of 7 to 10 days

at the new lower temperature, little further decrease in association with the bottom occurred.

Contact with solid objects has frequently been put forward as a possible means of position maintenance by stream fishes in the dark (Lyon, 1904; Hoar, 1951, 1954). Night observation (infra-red viewing apparatus) at Inlet Creek of temporary positive reorientation and maintenance of position by fry moving downstream upon touching or approaching solid objects suggests that tactile stimuli may be of importance in this respect. If so, then it seems reasonable that the increased direct contact with the bottom shown in the dark by fry held at 15 and 20° may, in part at least, account for their increased ability to maintain position in the dark at higher water temperatures, as demonstrated in streams of the Loon Lake system.

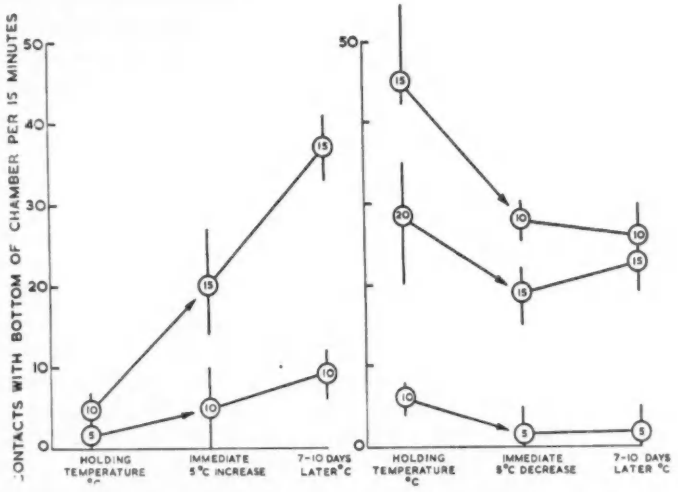

FIG. 21. Effect of temperature change on association with bottom by rainbow trout fry in experimental chamber in darkness. Circles and lines represent averages and ranges, respectively, of observations.

In summary, certain features of activity, depth distribution and contact with the bottom exhibited by fry in the above experiments all suggest that fry held at 15 or 20° should have less difficulty in maintaining their position in flowing water at night than fry held at 5 or 10°. Moreover, the few experiments on rapid and prolonged temperature change suggest that fry transferred to a higher or lower temperature would rapidly take on and retain behaviour characteristic of the new temperature.

2. SIZE AND DENSITY OF FRY

Experiments at Inlet Creek on downstream movement of different sizes of fry at night (Fig. 9B) suggested that larger fry (31–50 mm) may be more successful in maintaining position than small fry (21–30 mm). These exper-

iments, together with observations on disturbance of fry along the stream edge at night, suggest that size and density of fry may be of importance in affecting their ability to maintain position. Further laboratory experiments were not conducted in this direction.

MAINTENANCE OF POSITION BY FINGERLINGS

Considered on a seasonal basis, fingerlings in all streams of the Loon Lake system apparently maintain their position without appreciable movements downstream or upstream, throughout late autumn, winter and early spring. Experimental evidence presented previously (Fig. 14) suggests that short day length may be an important factor in restricting downstream movement of fingerlings and thus favouring maintenance of position during late autumn and winter months. Unfortunately no experiments were performed with short-day-length fingerlings at characteristic winter temperatures (5° or less). Failure of holding facilities at 5° eliminated the group of fish held for that purpose.

UPSTREAM MOVEMENT OF FRY

A. Characteristics of Upstream Movement

1. Seasonal periodicity

Trapping facilities capable of recording upstream movement of fry were operated for two seasons (1953, 1954) and during shorter periods in other years (1955, 1957, 1958) at Inlet, Hihium and Outlet Creeks. Upstream movement of fry was confined largely to the latter stream. Of 7,106 fry moving through Inlet Trap 2 between June and November of 1953, only 28 (0.39%) were moving upstream and of 82,684 fry moving through Inlet Trap 1 during the same period, only 309 (0.38%) were moving upstream. Similar amounts of upstream movement of fry were recorded at Hihium Trap 1 during a 3-month summer period of operation in 1954.

Seasonal periodicity of upstream movement of fry in Outlet Creek is shown in Fig. 22. Although free-swimming fry were present in Loon Outlet by early June in 1953, upstream fry movement did not begin until a month later at either trap location. Difficulty in maintaining traps because of high water prevented positive confirmation of this lag in movement in 1954, however operation of trapping facilities for periods in June and July of 1957 and 1958 showed it to be a characteristic feature of upstream fry movement in the outlet stream. Upstream movement of fry virtually ceased by early October.

2. Diel periodicity

Fluctuations in number of fry moving upstream over a 36-hour period were recorded at Outlet Traps 1 and 2 between July 23 and 24, 1953. Both traps were checked frequently, usually at 2-hour intervals or less throughout the 36 hours, and fry were counted and put upstream above the trap.

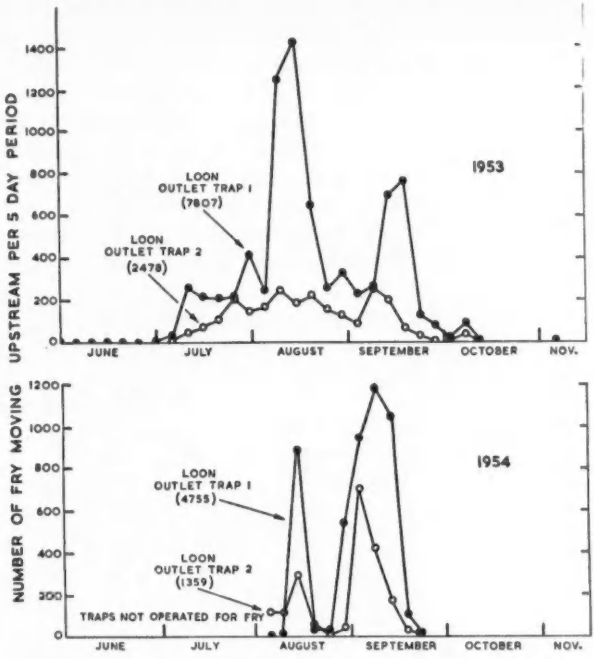

FIG. 22. Seasonal periodicity of upstream movement of rainbow trout fry in Outlet Creek. Numbers in brackets indicate total number of fry moving upstream during period shown.

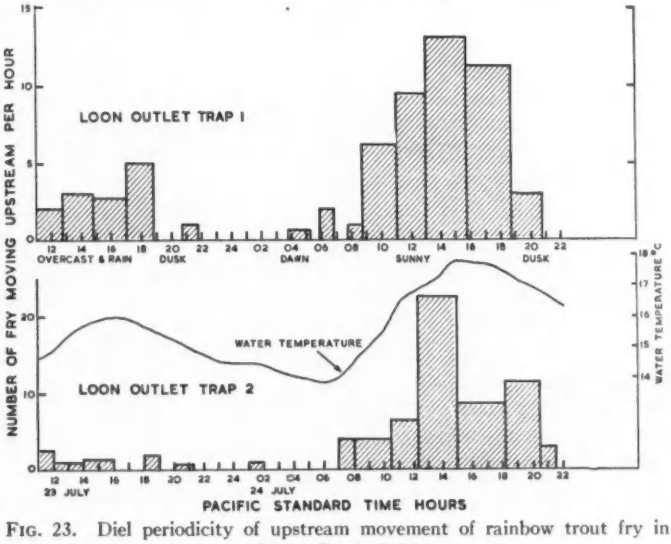

FIG. 23. Diel periodicity of upstream movement of rainbow trout fry in Outlet Creek, 1953.

Upstream movement of fry in Outlet Creek is largely confined to daylight hours (Fig. 23), although appreciable upstream movement does not begin until several hours after dawn. The start of upstream movement each day appears to follow the midday rise in water temperature more directly than the rapid changes in light intensity occurring at dawn (Fig. 23). Upstream fry movement reaches a maximum during early afternoon, as do stream temperatures, and gradually declines in late afternoon to virtual cessation at or shortly after dusk. Diel periodicity of upstream fry movement at Outlet Creek at other times throughout the 1953 season was similar to that recorded in detail between July 23 and 24.

Although very few fry moved upstream at Inlet Creek, some information is available for several 24-hour periods (Table IV). As at Outlet Creek most fry moved upstream during the afternoon.

TABLE IV. Number of fry moving upstream in several 24-hour periods at traps on Inlet Creek.

Time Period (Standard Time)	Inlet Trap 2 August 3–4 1953	Inlet Trap 1 August 3–4 1953	Inlet Trap 1 August 11–12 1954	Inlet Trap 1 August 12–13 1954	Total
Morning (0400–1200)	2	2	14	4	22
Afternoon (1200–2100)	6	3	25	18	52
Night (2100–0400)	3	0	8	6	17

3. DAILY PERIODICITY

Marked day-to-day fluctuations occurred in numbers of fry moving upstream through Outlet Traps 1 and 2. (Figure 23 shows differences between two consecutive days in July, 1953.) However daily trap catches could not be taken directly as a measure of the total number of fry moving upstream throughout 24–hour periods. In the first place, it was not possible to service traps at the time of minimum overlap between runs of successive days (i.e. between 2400 and 0400 hours; see Fig. 23). Furthermore traps were not always attended at regular intervals, so that catches on some days represented upstream fry movement for more than 24 hours, while on other days considerably less.

Recorded "daily" fry catches were adjusted to 24–hour (0000–2400 hours) catches by the following method:

1. Diel periodicity of fry catch at Outlet Trap 1, July 24, 1953 was taken as a standard and expressed as hourly percent of total numbers accumulated throughout the 24-hour period.
2. Where catches of two or more successive days were confounded, the total catch was apportioned on the basis of accumulated percentage catch pertaining to each day in the interval between trap servicing.

This method assumed that diel periodicity of July 24 was representative for the whole season of upstream fry movement, an assumption borne out in general by observation throughout 1953 and during 1954 and 1955. Also, in dividing a catch between two successive days it was assumed that *total* catch was the same on each day. This assumption introduced little error where only a small percentage of the second day's catch would have accumulated, that is, in cases where the trap was serviced before noon of the second day (see Fig. 23). Usually both Outlet Traps 1 and 2 were serviced each day in the morning, so appreciable error from this source only occurred on a few days during the season.

Calculated daily upstream movement of fry at Outlet Trap 1 is shown in Fig. 24. Considered on a day-to-day basis, upstream movement of fry appears to be characterized by irregular "surges". For periods of several consecutive

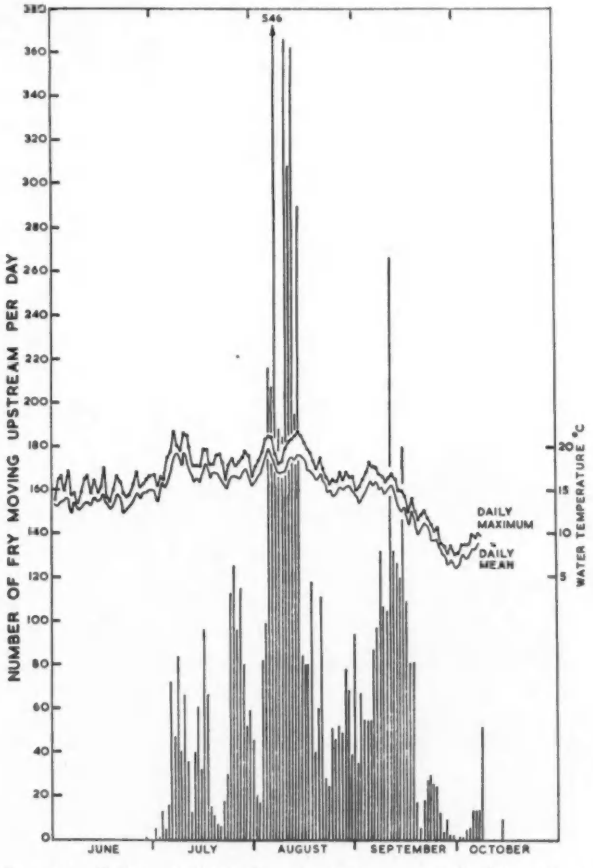

FIG. 24. Daily periodicity of upstream movement of rainbow trout fry in Outlet Creek (Outlet Trap 1), 1953.

days numbers moving upstream rapidly increased, and then fell off once more to a level below 30 per day. This feature of upstream fry movement was especially evident at Outlet Trap 1 (Fig. 24), but was followed with approximately similar timing at Outlet Trap 2 (data not shown).

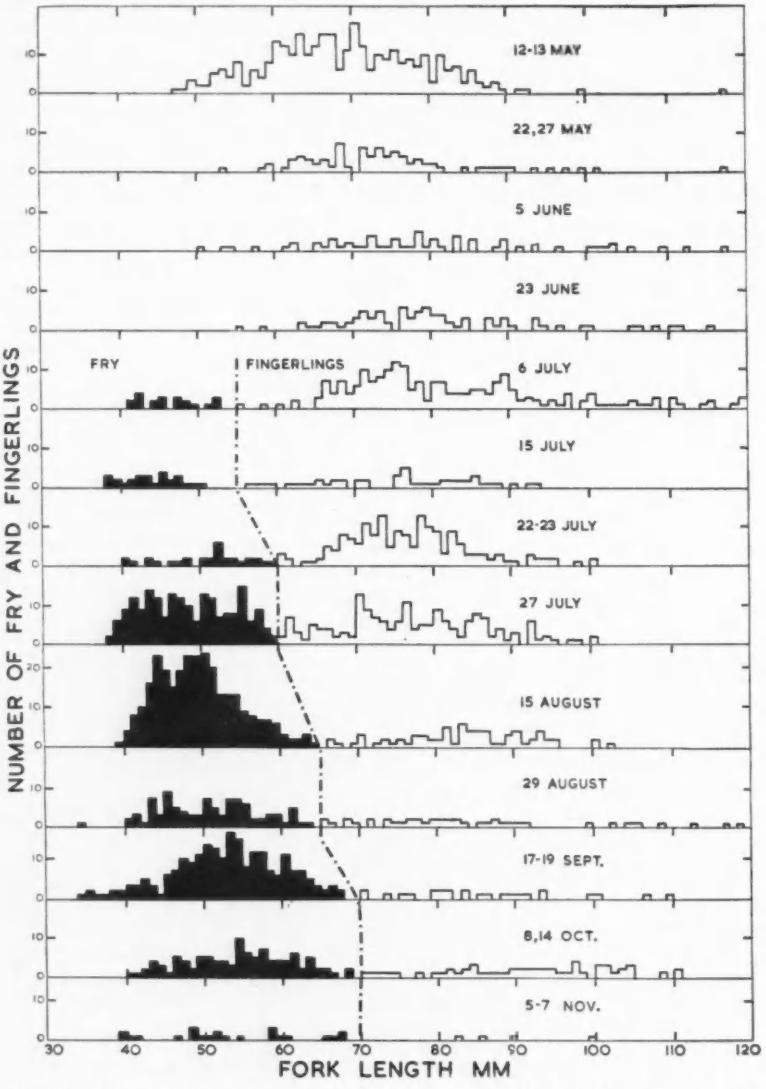

FIG. 25. Length-frequency distribution of rainbow trout fry and fingerlings moving upstream into Outlet Trap 1 during 1953.

4. Size relationships

Periodically, samples of young trout moving upstream through Outlet Traps 1 and 2 were measured during the summer and autumn of 1953. Results of these measurements are given in Fig. 25 for Outlet Trap 1. Fry were readily distinguished from young of the previous year class throughout early July, but large fry began to overlap the fingerling size range by late July. The most suitable length separating the two groups was chosen on the basis of these samples and used in the field during periods between sampling to distinguish between ascending fry and fingerlings. The same length division was used at Outlet Traps 1 and 2.

Although fry in Outlet Creek emerge free-swimming from the gravel at lengths between 20 and 25 mm, individuals less than 33 mm never ascended into either outlet trap in 1953. Water velocity at the upstream entrance to Outlet Traps 1 and 2 varied considerably depending upon stream discharge and state of plugging of the screen fence. However even during periods of high stream discharge, average entrance velocities to ascender boxes probably did not often exceed 10 cm/sec. Fry maintaining position or moving upstream for any distance in Outlet Creek probably would encounter velocities greater than this at many points along the stream.

Samples of fry were taken by seining from Outlet Creek periodically throughout the summer of 1953. Length frequency distributions for these samples indicate that fry less than 30 mm long were present in Loon outlet Creek at least until late August, although none moved upstream through outlet traps. Most fry in Outlet Creek apparently do not move upstream for any considerable distance towards the lake until they attain a length greater than 40 mm.

B. Factors Affecting Upstream Movement

One of the most striking features in the upstream movement of rainbow trout fry in Outlet Creek is the occurrence of marked surges in daily numbers ascending the stream (Fig. 24). Consideration of factors which may be responsible for this characteristic of upstream movement could lead not only to a more complete understanding of upstream movement in the outlet itself but also may suggest reasons why such movement does not occur in other streams of the system.

Variations both in supply of fry "available" to move upstream and in favourability of environmental stimulation for upstream movement might contribute to the production of surges. As fry in Outlet Creek do not begin to move upstream immediately or shortly after emergence, even a detailed knowledge of numbers of recently emerged fry present in the stream from day to day would not be great value in determining numbers available to move upstream. However, it does not seem reasonable to postulate that supply alone is responsible for the large, rapid daily fluctuations which occur in numbers of fry ascending the outlet stream. Supply may contribute to seasonal periodicity of upstream movement but probably is of less importance in regulating day-to-day changes. Considering environmental factors which may be involved,

few exhibit fluctuations of a size or rapidity which might reasonably be correlated to surges. Field notes show that water level (and hence roughly discharge of Outlet Creek in 1953 followed a pattern similar to 1954 but with a lower maximum level. No marked day-to-day changes in level were observed.

1. Water temperature

(*a*) *Relationships in the field.* Figure 2 indicates that marked day-to-day changes in temperature of Outlet Creek do occur and suggests the possibility of a correlation between these changes and surges in upstream movement of fry.

At least 5 fairly distinct surges in upstream movement of fry through Outlet Trap 1 are evident in Fig. 24. Increasing and decreasing phases of these surges were considered in relation to daily changes in maximum outlet temperatures. Five out of 6 increasing phases were associated with periods of general increase in outlet temperatures, while all 5 decreasing phases of upstream movement occurred during periods of decrease in outlet temperature. A similar comparison was made for 3 distinct surges in upstream movement of fry at Outlet Trap 1 in 1954. The same relationship between phase of surge and temperature change was evident as in 1953 data. The highest daily numbers of fry moving upstream into Outlet Trap 1 in 1954 (891) was recorded on August 13, a day of sharp increase in maximum outlet temperature following a prior 10-day period of consistently lower water temperature (Fig. 2).

The relation between day-to-day fluctuations in numbers of outlet fry moving upstream and changes in outlet temperature was examined by regression analysis. Quantitative expression of fluctuation in upstream movement presented a difficult problem, largely because no data were available on number of fry present in the stream. As information on supply of fry available to move upstream could not be obtained, numbers moving on one day were expressed as a fraction of those which moved upstream the previous day. Four degrees were added to all temperature changes to avoid negative numbers. Data for 100 days between July 1 and October 8, 1953 at Outlet Trap 1 were treated using logarithmic transformation.

A significant positive regression ($P < 0.01$, correlation coefficient $r = 0.696$) was obtained between daily changes in maximum outlet water temperature and daily changes in number of ascending fry. The analysis indicated that there was a marked tendency for upstream fry movement to exceed that of the previous day when the maximum daily temperature was above that of the previous day, and likewise to drop below that of the previous day when the maximum daily temperature was lower than that of the previous day.

Outlet Creek, during the period of upstream fry movement (July to mid-September), is not only considerably higher in temperature than Inlet or Hihium Creek but also is subject to more rapid and extensive daily changes in maximum temperature (Fig. 2). Both the lower level of maximum daily stream temperatures and their reduced daily variation may contribute to the virtual absence of upstream movement of fry in Inlet and Hihium Creeks.

(*b*) *Experimental flume studies.* The two experimental flumes at the confluence of Outlet and Hihium Creeks (described on page 211) were used also to study effect of temperature on upstream movement. Although the fry used were smaller than those moving up Outlet Creek, nevertheless consistent differences were evident in positive response to current between fry held in the two flumes with differing temperatures (Fig. 10). Fry of both Inlet and Outlet stocks in the flume supplied with warm Outlet water in most cases showed appreciably more upstream movement than did fry in cool water from Hihium Creek. Upon transfer (night of August 8) to the Outlet flume, fry formerly held in the Hihium flume showed a marked increase in amount of upstream movement.

(*c*) *Experimental stream studies.* A number of experiments were conducted in the stream on upstream movement exhibited by trout fry held at 10° and at 15 and 18°. Procedure employed has been outlined previously. In the light, units of upstream movement recorded for fry held at the higher temperatures were consistently larger (usually more than double) than those for fry held at the lower temperature.

2. Light

Field observations at Outlet Creek have shown that upstream movement of fry is largely restricted to daylight hours (Fig. 23). In experiments performed in the experimental stream, upstream movement of fry virtually ceased at light intensities below 1 foot-candle. Available evidence, although not extensive, does suggest that daily cessation of upstream fry movement is regulated by light intensity.

UPSTREAM MOVEMENT OF FINGERLINGS

A. Characteristics of Upstream Movement

1. Seasonal periodicity

Figure 26 summarizes data obtained on seasonal periodicity of fingerling movement up Loon outlet Creek for two consecutive years. A similar pattern (not shown) of upstream movement was obtained on these same years at Outlet Trap 2, although fewer fingerlings were involved. The majority of fingerlings move up Outlet Creek between May and August each year.

Available information on upstream movement of fingerlings in Hihium Creek in 1954 and in 1955 indicates that very few individuals are involved. As known from clip recoveries, the occasional fingerling from Outlet Creek moves at least short distances up Hihium Creek.

Throughout the 1953 season very few fingerlings moved up Inlet Creek, except during a few days in mid-July when daily number of ascending fingerlings ranged from 14 to 43 individuals. Before and after this period, rarely more than 10 and usually only 1 or 2, if any, fingerlings moved upstream each day.

2. Diel periodicity

Diel changes in numbers of fingerlings moving upstream were recorded in Outlet Creek for several 24-hour periods when traps were checked at regular

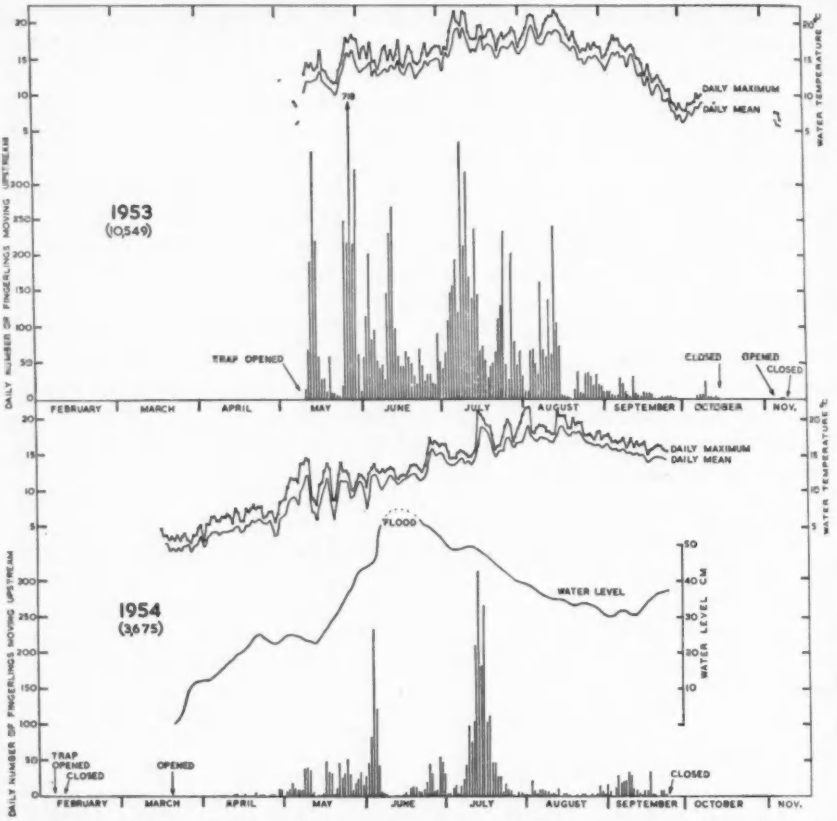

FIG. 26. Seasonal periodicity of upstream movement of rainbow trout fingerlings in Outlet Creek (Outlet Trap 1). Numbers in brackets indicate total numbers of fingerlings moving upstream during period shown.

intervals, usually about 2 hours. Data for both Outlet Traps 1 and 2 during a period in July, 1953, are shown in Fig. 27. Other less complete data on diel periodicity of upstream fingerling movement during 1953, 1954 and 1955 indicated a similar pattern.

The majority of fingerlings move upstream in mid to late afternoon during the daily rise to maximum stream temperature, however maximum rates of movement do not always occur during the period of daily maximum stream temperature, particularly at Outlet Trap 2. Upstream movement gradually decreases in the late afternoon and evening each day, reaching minimal rates in the early morning after dawn. Periods of minimal upstream movement occur near or during the period of minimal stream temperature.

Diel periodicity of upstream movement of fingerlings at Inlet Creek appeared similar to that at the outlet stream on the few days when appreciable upstream movement occurred at the inlet stream.

3. Daily periodicity

Expression of day-to-day changes in number of rainbow trout fingerlings moving up Outlet Creek is subject to similar difficulties outlined previously for daily upstream fry movement. Fingerling catches were adjusted in the manner described for fry, above, July 23–24, 1953, being taken as a standard (Fig. 27). The 24-hour interval beginning at 0700 hours was chosen as the most suitable "day's run". Assumptions and possible errors in the adjustment are the same as stated for fry.

Figure 26 shows that the "surges" in upstream movement observed in fry ascending Outlet Creek are also evident among ascending fingerlings in 1953 and 1954.

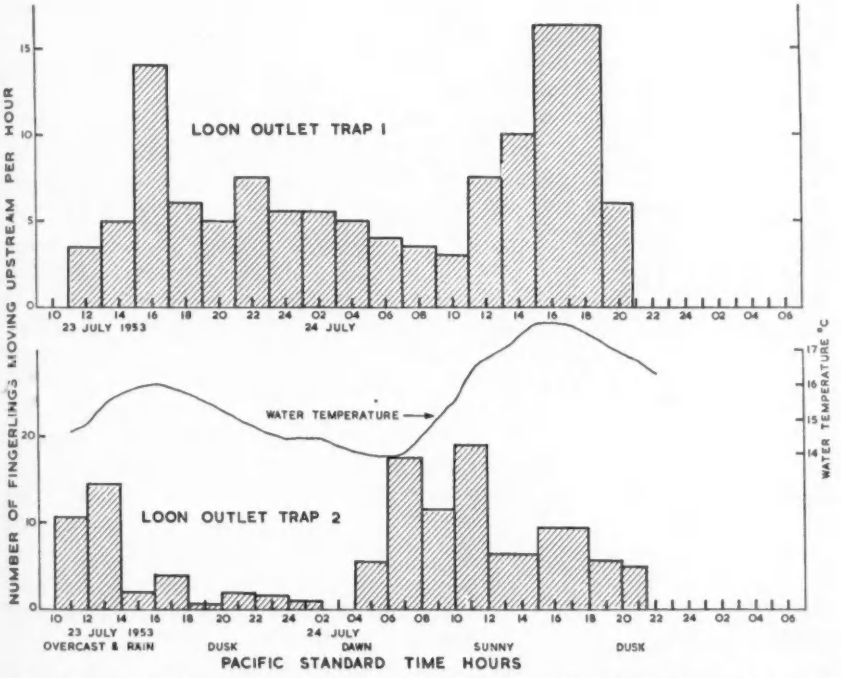

Fig. 27. Diel periodicity of upstream movement of rainbow trout fingerlings in Outlet Creek, 1953.

4. Size relationships

Seasonal changes in the length-frequency distribution of fingerlings ascending through Outlet Trap 1 are shown in Fig. 25. Distinction between fry and fingerlings during mid-summer and autumn has been mentioned previously. Comparison of late autumn fry and spring fingerlings suggests that the majority of fingerlings ascending Outlet Creek in late spring and summer are entering their second year of life. At least some of the larger fingerlings may have spent two or more winters in the outlet stream.

B. Factors Affecting Upstream Movement

1. Water temperature

(*a*) *Relationships in field.* Each of 6 increasing phases of surges in upstream fingerling movement in Outlet Creek in 1953 were associated with periods of rising daily maximum stream temperature, while the decreasing phases of the surges in movement occurred during periods of little temperature change or dropping daily maximum temperatures. Similar trends were evident for many of the minor surges in upstream movement shown in Fig. 26.

The relation between daily changes in water temperature and number of fingerlings ascending Outlet Creek was made by regression analysis using logarithmic transformation. Data were available on 60 days between May and August, 1953. Analyses were made for two expressions of change in daily maximum stream temperatures: (a) maximum of one day compared to that of the previous day and (b) maximum of one day compared to the average of the maximums of the two previous days.

A significant positive regression ($P < 0.05$, correlation coefficient $r = 0.293$) was obtained for the analysis with (a); that for (b) was highly significant ($P < 0.01$, correlation coefficient $r = 0.397$). Daily changes in upstream movement of fingerlings in Outlet Creek, as was shown previously for fry, can be related to changes in daily maximum water temperature.

In consideration of environmental factors possibly responsible for the marked differences in numbers of fingerlings moving up streams of the Loon Lake system, one must recall that it is only in Outlet Creek that fingerlings are abundant. In both Inlet and Hihium Creeks the majority of young leave the streams as fry and few apparently successfully over-winter in these streams. Nevertheless, differences in fingerling abundance between the streams may not be the only cause of their differences in amount of upstream movement of fingerlings. Figure 26 shows that periods of active upstream movement in Outlet Creek are generally associated with rises in maximum daily stream temperatures which approach or exceed 15°. Comparison of temperatures for all 3 streams (Fig. 2) shows that only during one period in 1953 did maximum temperatures at Inlet Creek exceed 15°. It was *only* during these few days in mid-July when an appreciable amount of upstream movement in fingerlings was recorded at Inlet Creek.

2. Combined effect of temperature and light

Information on the effect of 3 different temperatures (10, 15 and 20°) and 2 day lengths (8 and 16 hours) on the upstream movement of fingerling rainbow trout was available from observations made as described for downstream movement (page 232). Figure 28 shows that only for fingerlings held at 10° were there consistent differences in upstream movement of the 8- and 16-hour groups. There a positive reaction to current was expressed in at least 2 of the 3 groups tested which had been held at 8-hour day length. Those held at the combination of low temperature and long day showed less upstream movement than any other group tested in the experimental stream.

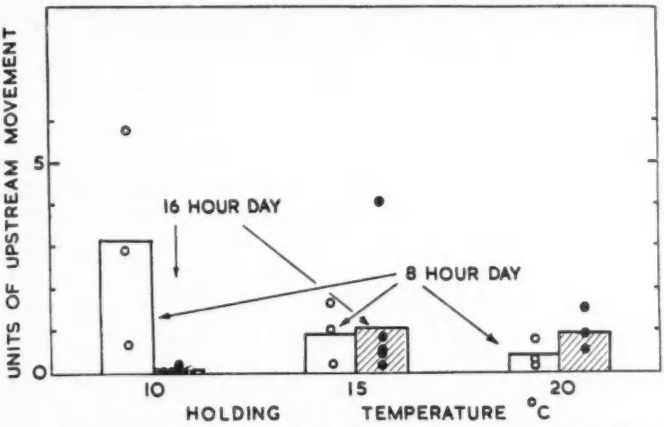

FIG. 28. Upstream movement exhibited in experimental stream by rainbow trout fingerlings held at different combinations of temperature and day length. Dots represent individual lots; columns are averages.

Thus fingerlings held at low temperatures and with short days exhibit moderately strong positive rheotaxis — a behaviour feature which might well be of importance to fish attempting to maintain position in a stream during autumn and winter. However, with the higher water temperatures and long days which characterize late spring and summer at Outlet Creek, no marked tendency for increased upstream movement was observed.

The effect of immediate and prolonged temperature change on upstream movement in the experimental stream was tested for several groups. One group of 5 fingerlings which had been held at 8-hour day and two groups at 16-hour day length were tested at each temperature. Responses to current were recorded on 10 or more separate 5-minute periods with each group, using the methods of previous experiments (page 232).

With a 5° temperature increase, an increase in upstream movement followed each increase, at both day lengths and both temperature changes (Fig. 29). Increase in upstream movement was greatest after 24 hours at the new higher temperature in both groups of 8-hour-day fish and in one of two groups of 16-hour-day fish. Upstream movement decreased in all groups after 72 hours at the new temperature.

The effect of a 5° decrease in temperature on upstream movement was examined only in 16-hour-day fingerlings. Experimental procedure was the same as in temperature increase tests except for the 5° decrease, which required about 2.5 hours. In groups of fingerlings showing some upstream movement (those at 20°), this movement was reduced markedly following the 5° decrease in temperature.

Although laboratory study on effects of temperature change on upstream movement of fingerlings was not extensive, nevertheless in all experiments a marked alteration was noted in upstream movement following both increases

and decreases of temperature. *Changes* in temperature produced greater alterations in positive response of fingerlings to water current than were noted between different combinations of *constant* holding temperature or day length. The direction of alteration in current response of fingerlings in the experimental stream was the same as noted between temperature change and upstream movement in Outlet Creek. In each situation, increases in upstream movement were related to periods of increasing water temperature and declines in upstream movement to decreasing water temperature.

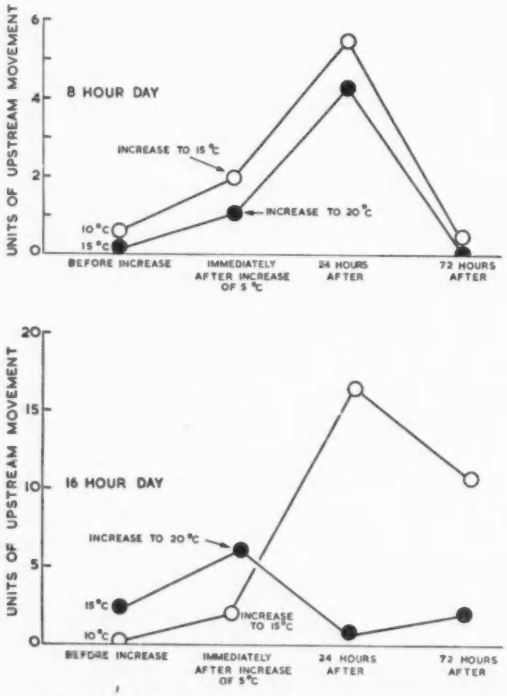

FIG. 29. Effect of 5° increase in temperature on upstream movement in experimental stream of fingerling rainbow trout held at 8- and 16-hour day length. Circles indicate averages for all lots tested.

MIGRATORY PATTERNS IN OTHER STREAM SYSTEMS

A. SIXTEEN MILE LAKE OUTLET

A survey was made of available data on migratory patterns shown by juvenile rainbow trout in outlet and inlet streams of lakes other than Loon. The most complete set of data examined was for upstream movement of fingerling trout in the outlet stream of Sixteen Mile (Baker) Lake — a small lake near Quesnel, B.C., 42 acres (17 ha) in extent. Observations on daily periodicity

of upstream fingerling movement, water temperature and level collected by the British Columbia Fish and Game Branch are presented in Fig. 30. Some, but probably by no means all of these young trout were progeny of adults inhabiting Baker Lake and spawning in its outlet stream. An unknown fraction may have been progeny of adults either inhabiting the outlet stream or other lakes lower in the system. Diel periodicity of upstream movement on all 3 years was shown to be very similar to that at Loon Lake. Most fingerlings ascended the outlet stream in mid-afternoon and very few during the night and early morning.

Movement of fingerling trout in appreciable numbers up Baker Lake outlet stream began, at least in 1956 and 1957 (Fig. 30) after the first sharp *rise* in outlet temperature to levels above 10° (daily mean). Increase in both daily stream temperature and number of ascending fingerlings appeared to be more gradual in 1958 than in the previous years. Several surges in upstream movement were evident in 1956 and 1957 data (Fig. 30). In most cases increasing and decreasing phases of each surge were associated with periods of general increase and decrease in daily maximum water temperature. In the year (1958) when no marked periods of temperature increase and decrease occurred, little evidence of surges in upstream fingerling movement was found. Fluctuations in water level did not appear to affect numbers of fingerling trout ascending Baker Lake outlet stream. The relation of seasonal, daily and diel periodicity of upstream movement to changes in water temperature at Baker Lake outlet stream was similar to that observed at the outlet of Loon Lake.

B. Wasilla Lake Outlet

Data were examined on upstream movement of rainbow trout less than 7 inches (18 cm) at the outlet weir of Cottonwood Creek (outlet stream of Wasilla Lake, Alaska) given in Job Completion Report Vol. 8, No. 4, U.S. Fish and Wildlife Service Project F-I-R-8, Alaska, 1959. Plotting daily average water temperatures of the outlet stream on the graph showing daily upstream movement of young trout showed a relation between surges in upstream movement and changes in water temperature similar to that found at outlet streams of Loon and Baker Lakes. Each of the 4 major periods of increase and decline in numbers of trout ascending the outlet stream of Wasilla Lake was associated with respective periods of increase and decrease in stream temperature.

C. Paul Lake Inlet

Downstream migration of rainbow trout fry in Paul Creek, an inlet to Paul Lake near Kamloops, B.C., has been observed by Mottley (1931b) who estimated that 15,000 fry entered the lake from Paul Creek during the summer of 1931. In 1952 the British Columbia Fish and Game Branch operated a Wolf-type fry trap on Paul Creek a short distance upstream from its entrance into the lake where data on downstream movement of fry and stream temperature were obtained. Downstream movement of fry occurred throughout most of the period between installation of the trap (July 20) and the end of August when low water level prevented its effective operation. During the

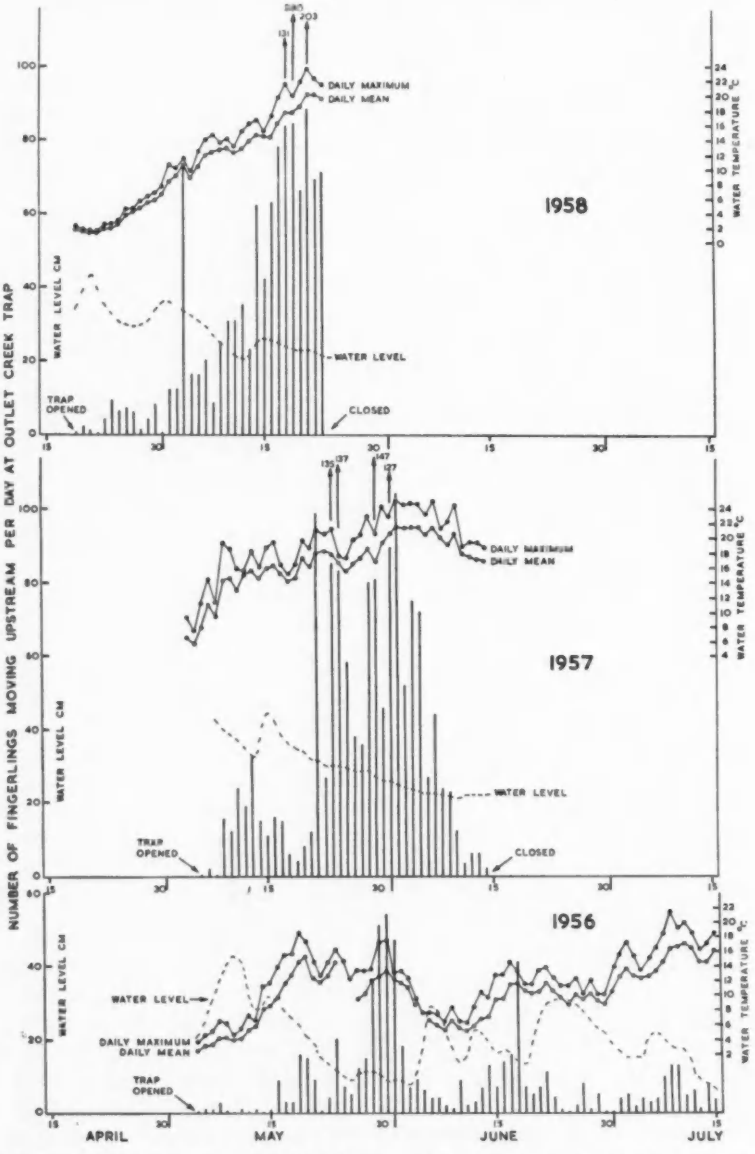

FIG. 30. Upstream movement of rainbow trout fingerlings at trap on outlet stream of Sixteen Mile (Baker) Lake, B.C.

43-day period, mean daily stream temperature was less than 13° on 25 days and only exceeded 14° on 4 days. Thus throughout most of this summer period the temperature of Paul Creek remained within the range at which downstream movement of fry occurred in Loon Lake streams.

D. Lardeau River

Some information on migratory behaviour of young rainbow trout resulting from spawning of large adults from Kootenay Lake in the Lardeau River is available (Larkin, 1951; Cartwright, 1961; and unpublished data of the British Columbia Fish and Game Branch). Lardeau River, approximately 30 miles in length, flows from the southeast end of Trout Lake into the north end of Kootenay Lake and thus at its upper end forms the *outlet* of Trout Lake but at its lower reaches an *inlet* of Kootenay Lake. Many of the large rainbow trout spawning in the river do so near its upper end a short distance below Trout Lake. Emergence of fry extends from mid-June in the upper reaches to early August in the lower reaches of the river.

Arguing from the effect of water temperature on migratory behaviour of juvenile rainbow trout at Loon Lake, one would predict the following pattern of fry movement from an examination of seasonal changes in temperature (1949, 1958, 1959) of the Lardeau River at several points along its length:

(a) Most fry emerging in late June to early July would move downstream at night towards Kootenay Lake.
(b) Most fry emerging in the upper reaches after early July would not move downstream at least during most of July, August and early September.
(c) Some fry in the upper reaches in late July and August would move upstream towards or into Trout Lake during the day.
(d) Many fry emerging in the middle and lower reaches throughout the summer would move downstream towards Kootenay Lake.

Although data on movement of juvenile trout in the Lardeau River are not extensive, the following statements can be made on the basis of fyke netting, scoop trap operation and other observations:

(a) After the beginning of emergence and until early July considerable numbers of fry do move downstream at night.
(b) Although some downstream movement of fry continues in reduced numbers during later July and August in the upper reaches, many fry apparently maintain position day and night in this section of the river at least until early September.
(c) Although upstream movement of fry in the upper river towards or into Trout Lake has not been positively recorded, R. McRae, retired hatchery officer for the B. C. Fish and Game Branch, reported (personal communication) that considerable numbers of rainbow trout fry are seen during the summer along the shores of Trout Lake immediately above the mouth of Lardeau River and that in his opinion many fry do move from the uppermost reaches of the river into Trout Lake.
(d) Downstream movement of fry in lower reaches is known to occur during July and August.

The observed pattern of migratory behaviour of juvenile trout in the Lardeau River is reasonably consistent with predictions based on environmental control of movement at Loon Lake.

In summary, available information has been examined on migratory behaviour of juvenile rainbow trout in four widely separated systems, representing two outlet streams, one inlet stream and a single river which at its upper end forms an outlet stream and at its lower end becomes an inlet stream. In each case, observed migratory behaviour is, in general, consistent with that which would have been predicted on the basis of the Loon Lake study.

DISCUSSION

A. Environmental Control of Current Responses

Three major categories of response to water current have been recognized in the migratory behaviour of juvenile rainbow trout in streams of the Loon Lake system. A summary of observations in the field and pertinent field and laboratory experiments is given below. Numbers in brackets at the end of each item of experimental evidence indicates its pertinence to particular field observations:

Field observations	Experimental evidence
A. Downstream movement of fry	
1. Occurs consistently each summer in both streams (Inlet and Hihium) characterized by daily mean water temperatures $<13°$ but different in many other physical, chemical and biological aspects.	(a) Fry which had moved down Inlet Creek (at mean temp. $<10°$) virtually ceased such movement when transferred to Outlet Creek (at mean temp. $>15°$), while inlet control fry continued moving down inlet stream. (1, 2, 3)
2. Does not occur in Outlet Creek in summers when daily mean water temperatures are usually $>14°$.	(b) Fry which had exhibited little movement down Outlet Creek (at mean temp. $>20°$) moved downstream in relatively greater numbers when transferred to Inlet Creek (mean temp. 14.4° or less). (1, 2, 3)
3. Occurs occasionally in early summer in Outlet Creek when daily mean water temperatures are considerably $<14°$ for several days.	(c) Fry held in identical experimental flumes usually showed more downstream movement in flume supplied with Hihium Creek water (mean temp. $<12°$) than in flume supplied with Outlet Creek water (mean temp. $>15°$). (1, 2, 3)
	(d) In several types of tests at low light intensities in the experimental stream, fry reared or held below 15° consistently showed more downstream movement than fry reared or held at $>15°$. (1, 2, 3)
4. Takes place almost entirely at night when illumination falls below 0.01 foot-candle.	(e) Fry held in experimental stream at 10° and >1 foot-candle of illumination show considerable increase in amount of downstream movement when light gradually lowered to levels of and below 0.01 foot-candle. (4)

Field observations	Experimental evidence
A. Downstream movement of fry—Continued	
5. Amount and periodicity on any one night markedly affected by changes in intensity of nocturnal illumination (cloud-cover, moonlight).	(f) Changes in illumination below 0.01 foot-candle increase amount of downstream movement of fry in experimental stream. (5)
	(g) Downstream movement of fry at night greatly reduced during periods of lantern illumination over streams. (5)
6. Majority of fry involved range between 20 and 30 mm. in length, although considerable numbers of larger fry may be present in stream.	(h) Release and recovery of marked small (20–30 mm.) and larger (31–50 mm.) fry at Loon inlet Creek indicates that smaller fry move downstream to a greater extent and more rapidly than larger fry. (6)
B. Downstream movement of fingerlings	
1. Relatively small numbers involved in any of streams studied; largely confined to late spring and early summer (long day length) periods in streams with low daily mean temperature (usually $<13°$).	(a) Fingerlings held at 10° and long day length (16 hours) exhibited much more downstream movement in experimental stream than did those held at 20° and long day length. (1)
2. Not evident during autumn, winter or early spring in *any* of streams studied.	(b) Fingerlings held at short day length (8 hours) exhibited virtually no downstream movement in experimental stream. (2)
C. Maintenance of position by fry	
1. Above observations (1, 2, 3) on inability of fry to maintain position in streams are pertinent here.	(a) Above experimental evidence (a, b, c, d) on inability of fry to maintain position in flowing water is pertinent.
2. Fry maintain position at night in Outlet Creek when daily mean temperature $>14°$ but do not do so there when considerably $<14°$ or in other streams characterized by summer daily mean temperatures $<13°$.	(b) Fry reared at 15 and 20° show less horizontal movement during night than during day in experimental chamber, while those reared at 5 and 10° showed more horizontal movement during night than during day. (2)
3. Many of fry maintaining position at night do so along margin of stream in close proximity or occasional contact with solid objects along stream edge and bottom.	(c) Fry reared at 15 and 20° were more frequently recorded near bottom and made more frequent contact at night with bottom of experimental chamber than did fry reared at 5 and 10°. Latter group in darkness swam in current near or at surface of experimental chamber. (2, 3, 4)
4. Most of fry unable to maintain position at night swim erratically in disoriented manner at or near water surface away from stream edge or bottom.	(d) Fry transferred into water 5° higher or lower in temperature rapidly assumed response to bottom of experimental chamber characteristic for new temperature. (2, 3, 4)

Field observations	Experimental evidence
D. Maintenance of position by fingerlings	
1. Maintain position throughout most of winter and early spring in all streams studied.	(a) Fingerlings held at short day length (8 hours) exhibited virtually no downstream movement in experimental stream. (1)
	(b) Fingerlings held at short day length (8 hours) and lowest temperature (10°) showed strongest positive rheotaxis in experimental stream. (1)
E. Upstream movement of fry	
1. Occurs consistently each summer only in Outlet Creek where daily maximum water temperatures >15°.	(a) Fry held in identical experimental flumes usually showed more upstream movement in flume supplied with Outlet Creek water (mean temp. >15°) than in flume supplied with Hihium Creek water (mean temp. <12°). (1, 2)
2. Does not occur in Inlet Creek or Hihium Creek where summer daily maximum water temperatures rarely approach or exceed 15°.	(b) Fry held for several days at 18° usually exhibited more upstream movement when tested at that temperature in experimental stream than did fry reared and tested at lower temperature (10°). (1, 2)
F. Upstream movement of fingerlings	
1. Occurs consistently each year only in Outlet Creek during late spring and summer when daily maximum water temperatures approach or exceed 15°, and fluctuate considerably from day to day.	(a) Fingerlings held under *constant* day length *and* temperature conditions, even those with long day and high temperature, did *not* exhibit strong positive reactions to water current in the experimental stream. (1–4)
2. Does not occur in Hihium Creek where daily maximum water temperatures rarely approach 15° and do not show marked day to day fluctuation.	
3. Occurs to a limited extent in Inlet Creek on few days in midsummer when daily maximum water temperatures approach or slightly exceed 15°.	(b) Fingerlings held at moderate temperatures (10, 15°) and either 8-hour or 16-hour day showed an immediate increase in upstream movement in experimental stream when subjected to a 5° increase in temperature. Decreases of 5° resulted in an immediate decrease in amount of upstream movement shown previouslv. (4)
4. Fluctuations in daily numbers of fingerlings moving up Outlet Creek correlated with rapid and extensive fluctuations in daily maximum water temperature.	

The above presentation shows that experimental evidence corroborates field observations indicating environmental rather than genetic control of current responses.

B. Factors Involved In Control

In the case of juvenile trout during their first summer and autumn, three factors (water temperature, light intensity and size of fry) appear to be largely responsible for their different patterns of movement shown in streams of the Loon Lake system.

Water temperature is responsible, in large part, for differences in migratory pattern of fry *between* streams of the Loon Lake system and is involved in control of both seasonal and diel periodicity of movement *within* any one stream. Water temperature in the summary above has been expressed as daily mean with reference to downstream movement and maintenance of position, but as daily maximum with respect to upstream movement. In the former two types of behaviour a more general expression of temperature level seemed to be involved while in the case of upstream movement both diel and daily periodicity of movement had shown the best relationship with daily maximum temperatures.

Light intensity, in contrast to water temperature, does not bring about differences in response of fry to water current *between* streams but instead regulates diel periodicity of these responses *within* particular streams. Thus, in streams which do have daily mean water temperatures consistently below 13° in the summer (such as Inlet or Hihium Creek), timing of downstream movement each night is controlled largely by fall and rise of light intensity in the 0.01 foot-candle level. The marked decline in numbers of fry moving upstream with approach of dusk suggests that light intensity may regulate cessation of upstream movement each day.

Several marked changes and differences in migratory behaviour were associated with size of fry, both in outlet and inlet streams. The fact that most fry involved in downstream movement were less than 30 mm in length whereas numerous larger fry were present indicated operation of a "size factor" in downstream movement and maintenance of position. Experiments at Inlet Creek (Fig. 9B) clearly demonstrated an effect of fry size on downstream movement. Moreover, a marked change (onset of upstream movement) in current response of fry was noted at Outlet Creek as fry approached 40 mm in length. That fry less than 40 mm were physically incapable of moving up Outlet Creek does not seem probable in consideration of experiments performed on the swimming speeds of 40-mm rainbow trout fry acclimated to 10 and 20°. Some data from these experiments were given in Bainbridge (1958) which showed that 40-mm fry could swim, for several seconds at least, at speeds well in excess of 30 cm/sec. Smaller fry demonstrated swimming speeds approaching the above which would permit them to move up most stretches of Outlet Creek.

Some factors, such as water temperature, which are of importance in control of migratory patterns of rainbow trout fry in streams also appear to have similar effects on movements of fingerlings. Differences in migratory behaviour between streams as well as certain aspects of seasonal and diel periodicity of movement (particularly upstream) probably are controlled in fingerlings, as in fry, by differences in water temperature. Discrete diel periodicity in both upstream and downstream movement associated with changes in light intensity was not

so apparent in migratory behaviour of fingerlings as in fry. Laboratory experiments showed that day length had a marked effect on current response of fingerlings. Downstream movement was greatest at long day length and low temperature, agreeing well with field conditions under which downstream movement of fingerlings was most pronounced. Positive rheotaxis under experimental conditions was highest at short day length and low temperature — a response which possibly would be of importance in maintenance of position in streams from late autumn to early spring.

C. Mechanism and Interaction of Factors

Virtually all fry and many fingerling trout which move down streams of the Loon Lake system do so during nocturnal periods of low light intensity. Direct observation in the field and experimental evidence both in the field and laboratory indicate that downstream movement of juvenile rainbow trout in water current results from inability or difficulty in maintaining sensory reference to spatial surroundings at low light intensities. Reduction in visual association and actual contact with the bottom is brought about when fry move towards or to the stream surface, a behaviour which in young trout is markedly affected by temperature. A similar mechanism has been proposed (Hoar 1953, 1954, 1958) for nocturnal migrations of several species of juvenile salmon down streams. In these cases no marked temperature effect on association of fry with stream bottom was noted.

The sudden onset of downstream movement of trout fry each evening (Fig. 5, 6, 7) may be a result of a slow rate of dark adaption of the trout eye in relation to the concomitant rapid decrease in light intensity. Information on cone and rod threshold at low light intensity or on rate of dark adaption of the rainbow trout eye is not available. However, these values may be in the same order as those for several species of *Oncorhynchus* determined by Ali (MS, 1958). In salmon fry cone thresholds in the 1 to 0.1 foot-candle range were reported, with complete dark adaption requiring about 40 minutes. Rod thresholds, below which little or no visual orientation would be possible even after complete dark adaption, were given as 0.0001 foot-candle for 4 species of salmon (sockeye, coho, pink and chum). Hoar (1953) and more recently Ali (MS, 1958) suggested that "the marked peak in the downstream migration of the juveniles at dusk" may be due to the "state of partial night-blindness" occurring between the time when light intensities fall below the cone threshold and when the eye is fully dark adapted. Reduction or cessation of downstream movement may occur after complete dark adaption of the eye, provided illumination does not fall below 0.0001 foot-candle. Coincidence of timing in rapid onset of downstream movement of sockeye smolts in Lakelse River with rapid decrease in light intensity and features of dark adaption of the sockeye smolt eye has been noted by Brett and Ali (1958). Ali and Hoar (1959) have demonstrated a similar relationship for young pink salmon in both field and laboratory experiments. Field readings taken at the surface of Loon Inlet Creek (Figs. 6 and 7) and data presented by Dice (1945) show that intensities of nocturnal illumination do fluctuate below and above the 0.0001 foot-candle level on a

single night. Such fluctuations may be responsible for irregular changes recorded in numbers of trout fry moving down streams of the Loon system on several nights.

Although loss of visual contact with stream bottom at low water temperature is paramount in the mechanism of downstream migration, other factors may be involved. Lateral movement of fry into shallow water along the stream margin each evening prior to downstream migration results in a pronounced concentration of fry in a narrow band at edges of the stream. Numbers and size of fry competing for suitable holding areas may affect the extent of downstream movement exhibited by these young fish.

The fact that many of the fry moving downstream at night were actively "heading" downstream rather than drifting passively with the current may, in part, be associated with the disturbance of dense groups of fry along the stream margin. As suggested in Fig. 17, fry rapidly disperse laterally into the current and continue erratic swimming movements when disturbed by an individual entering the densely packed group from upstream. The majority of fry, in an effort to avoid the direction from which the intruder came may, initially at least, head out in a downstream direction.

Maintenance of position in daylight by juvenile trout is probably accomplished largely by visual reference points along the stream bottom or side. Classic experiments of Lyon (1904) and those of Schiemenz (1927) have demonstrated the importance of visual orientation in rheotactic responses of fish. Lowenstein (1957), reviewing the work of Dijkgraaf (1933) and others on function of the lateral line system in fishes considers that the chief mechanism of control of rheotactic orientation in darkness appears to be tactile stimulation. In summary Lowenstein (1957) states that:

> a fairly accurate three-dimensional sensory representation of the topographic features of the immediate environment, as well as the localization of moving objects in the vicinity, may thus be assumed to be mediated by this sense organ in the absence of visual orientation either in darkness or in a turbid medium.

Mechanisms of position maintenance by stream fishes in the dark, however, have not been carefully worked out in detail.

Hoar (1953) emphasizes the importance of territorial behaviour in prolonged residence of salmonids in streams and notes movement into shallow water, settling to the bottom and inactivity at night as behavioural characteristics associated with territoriality. Nocturnal observations in streams of the Loon Lake system show that lateral movement into shallow water in itself, does not lead necessarily to maintenance of position by juvenile trout. Large numbers of fry lost position at Loon Inlet Creek each evening following movement into shallow water along the stream margin. Laboratory observations on behaviour of fry in the dark under simulated stream conditions indicated that movement towards and repeated contact with the stream bottom may well be essential to maintenance of position. In no case, either in the field or in the laboratory, were juvenile trout seen to settle more or less permanently onto the stream bottom and remain inactive at low levels of illumination. Rapid re-orientation and temporary maintenance of position observed when fry moving downstream

struck or closely approached solid objects again emphasized the role played by tactile or pressure stimuli in the ability of young trout to hold position at night in flowing water.

Upstream migration of rainbow trout fry and fingerlings in streams of the Loon Lake system clearly seems to be regulated by water temperature. In this regard, temperature apparently has a two-fold action, (a) setting limits within which upstream movement may occur and (b) affecting intensity and timing of the response when it does occur. The mechanism involved has yet to be determined. Acceleration of metabolism and activity at higher temperatures may be involved in setting the temperature level above which upstream movement occurs, whereas sudden rises in temperature may act as a directing factor (Hoar, 1958) which brings about the reaction of swimming more strongly *into* water currents. A simple increase in activity coincident with rise in temperature, in itself, will not necessarily explain upstream movement, for this increased activity must be *oriented* in a specific direction.

Upstream migration of juvenile brown trout in the outlet stream of Lake Rensjön in Sweden (Runnström, 1957) apparently has a relation to water temperature similar to that in upstream movement of juvenile rainbow trout at Loon outlet Creek. Young brown trout only moved up Rensjön's outlet stream when its temperature exceeded 5–6°. Furthermore sharp increases in temperature above this level markedly increased daily numbers moving upstream while periods of constant or declining temperature were generally associated with reduction in numbers moving upstream. No statistical examination of the relation was made in this study. Limitation of upstream movement to water temperatures above a certain level was evident in the work of Sörensen (1951) on migrating elvers. Both in an experimental flume and in a number of Swedish rivers, elvers did not move upstream until the water temperature reached or slightly exceeded 15°.

Operation of water temperature as a factor directing or orienting movement with respect to water current was evident in the experimental studies of Keenleyside and Hoar (1954) on young salmon and those of Beauchamp (1937) on *Planaria alpina*. In the former study sudden rises in temperature of 4–5° brought about marked downstream swimming (negative rheotaxis) in both chum and coho fry but no alteration in current response of sockeye fry. Beauchamp's studies showed that introduction of planarians into water 5° higher than that in which they were living caused a positive rheotactic response in the animals. Hoar (1958) suggests that difference in response of sockeye fry to sharp rise in temperature, compared with chum and coho, may help explain the spectacular upstream migrations of large numbers of sockeye underyearlings in outlet streams of some lakes.

D. General Considerations

Considerable evidence has been presented for certain environmental factors, particularly temperature, playing a role in control of migration of juvenile rainbow trout in outlet and inlet streams of Loon Lake. A similar control was

suggested in several other stream systems examined. That temperature, of all factors which may direct or orient movement of fish in water current (Hoar, 1958; Collins, 1952), should predominate appears more reasonable when control of movement both upstream from an outlet and downstream from an inlet is considered. The one environmental factor which might be expected to differ consistently between inlet and outlet streams of most lakes, during observed migratory periods, is water temperature. Outlet streams, draining at most times water warmed at the lake surface, are probably warmer than their respective inlet streams throughout much of the year. Moreover they may be, at the same time, subject to rapid and extensive changes in temperature resulting from either sudden turbulent mixing by wind action of relatively thin layers of warmed lake water or by tilting and surfacing of deeper, cool layers of a lake in wind-induced thermal seiches so dramatically demonstrated by Mortimer (1952a, b). Such sudden changes in temperature would not be characteristic of most inlet streams, except where the outlet of one lake became the inlet of another in a relatively short distance. The importance of rapid *changes* in water temperature in affecting upstream movement of juvenile trout has been demonstrated both in the field and in controlled laboratory experiments.

Thus it seems probable that evolution of appropriate behaviour responses to water current by rainbow trout in order to ensure successful maintenance of lake populations, while exploiting all possible spawning facilities (both of inlet and outlet streams), has involved selection of a set of responses which are altered markedly by the most consistent environmental difference between these types of streams in the majority of lakes, namely their temperature characteristics.

CONCLUSIONS

1. Marked differences in water current responses of juvenile trout migrating into Loon Lake from outlet and inlet streams result from environmental differences between streams, rather than genetic differences between spawning stocks.
2. Differences in water temperature between Outlet and Inlet Creeks regulate differences in direction of migration through action on behaviour associated with downstream movement, maintenance of position and upstream movement.
3. At cool water temperatures (daily mean consistently $<13°$) recently-emerged fry exhibit little tactile association with the stream bottom; in darkness, they lose visual orientation and move downstream.
4. Maintenance of position in darkness by fry at warm temperatures ($>15°$) is facilitated by their frequent contact with the stream bottom.
5. Warm water temperatures (daily maximum usually $>15°$) in conjunction with sharp rises in temperature are associated with upstream movement of large fry (>40 mm in length); a similar relationship is evident in fingerlings.

6. Laboratory experiments suggest that combination of cool water temperature and *long* day length induces downstream movement of fingerlings; in the field, fingerlings move downstream under similar conditions (late spring and summer).

7. That combination of cool water temperature and *short* day length may facilitate maintenance of position by fingerlings is suggested by marked lack of downstream movement and slight positive rheotaxis shown by fingerlings tested in laboratory experiments under such conditions; in the field, fingerlings maintain position in streams under similar conditions (late autumn to early spring).

8. Evidence from 4 other widely separated stream systems indicates an environmental control of migration in juvenile rainbow trout similar to that demonstrated in the Loon Lake stream system.

9. Development of behaviour in current which would permit exploitation of both major types of spawning streams (outlet and inlet) by lake-dwelling rainbow trout has involved selection of responses markedly altered by water temperature, which is probably the single most consistent environmental difference between outlet and inlet streams of lakes.

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The Distribution of Animals in the Eastern North Pacific and its Relationship to Physical and Chemical Conditions[1, 2]

By William Aron[3]

ABSTRACT

Sampling with the Isaacs-Kidd midwater trawl yields good quantities of large and easily-identified animals that can be used as "indicator organisms" to identify water masses in the northeastern Pacific Ocean. Particularly useful are the myctophid fishes *Lampanyctus leucopsarus, Diaphus theta, Tarletonbeania crenularis, Electrona arctica, E. crockeri, Ceratoscopelus townsendi* and *Lampanyctus ritteri*, the pteropods *Limacina helicina, Cavolinia globulosa* and *Euclio pyramidata*, and the heteropod genus *Atlanta*. In going from Subarctic water to warmer Intermediate water in the open ocean, numbers of animals declined and the species changed markedly. By the time quantities of Central or Tropical water are encountered, catches were about $\frac{1}{100}$ of those in Subarctic water. Inshore catches off southern British Columbia and Washington in 1958 were only about $\frac{1}{10}$ as great as in comparable hauls in 1957 — a difference which coincides with a greater intrusion of Intermediate water in 1958.

INTRODUCTION

During the summer of 1957 and the summer and fall of 1958, the Department of Oceanography of the University of Washington conducted three cruises in the North Pacific aboard the research vessel *Brown Bear*. The first two of these cruises, Nos. 176 and 199, were part of the University's contribution to the International Geophysical Year. The third cruise, No. 202, was designed to investigate apparently anomalous oceanographic conditions detected off the Washington — British Columbia Coast during Cruise 199. The area studied ranged from about 32°N to 56°N and as far west as 174°E (Fig. 1a, b, and c).

On all three cruises the standard measurements of salinity, temperature, oxygen, and phosphates were made; bathythermograms were taken regularly along the cruise track; in addition, nearly 600 hauls were taken using modified versions of the Isaacs-Kidd midwater trawl. Some of the data obtained from the trawl hauls are analyzed in this report, with particular emphasis on the relationship which exists between the physical and chemical conditions and the resident biological populations. The physical and chemical data have been presented in Fleming (1958a, 1959) and in Love (1960).

The quantity of material taken with the midwater trawl is large and varied, both in number of individual animals and in number of major animal groups represented. Although complete analysis is impossible at this time, this report presents the progress made in studies of the material — particularly in regard to the fishes and to certain aspects of the planktonic regime.

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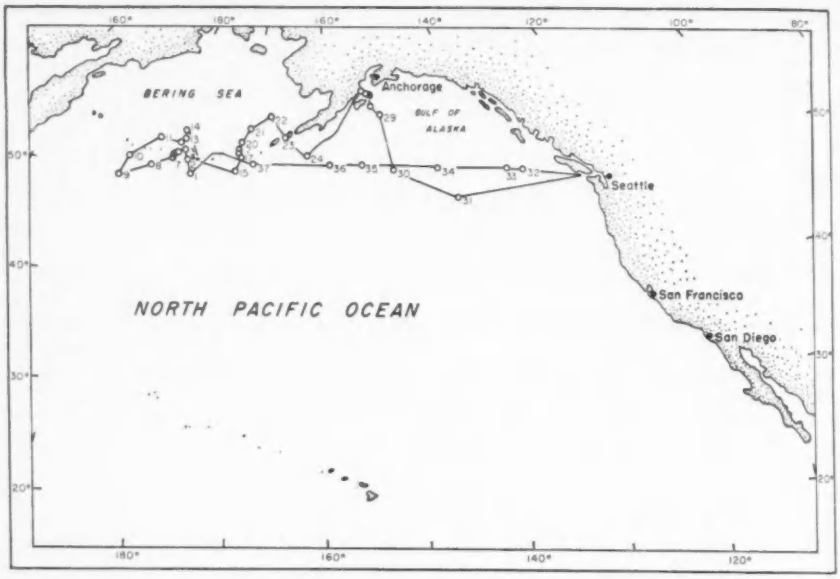

FIG. 1a. Cruise tracks showing hydrographic stations, *Brown Bear* Cruise 176.

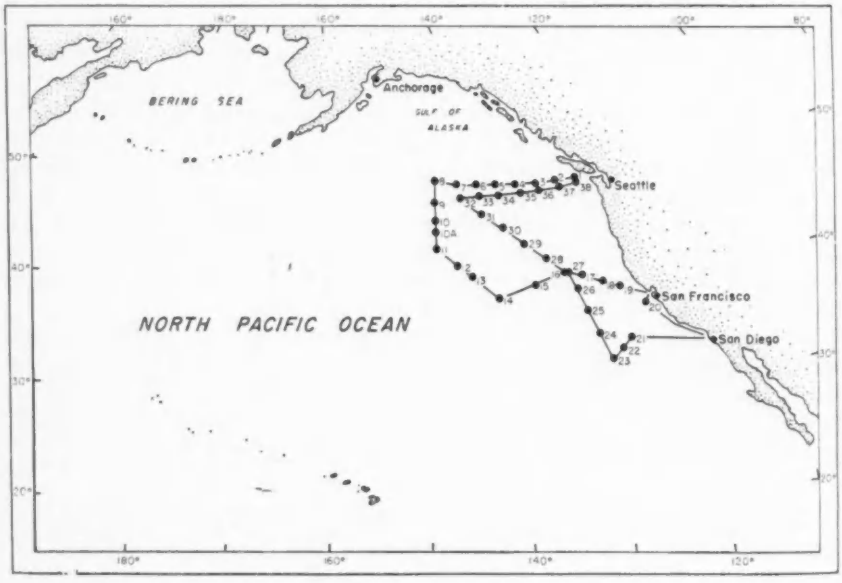

FIG. 1b. Cruise tracks showing hydrographic stations, *Brown Bear* Cruise 199.

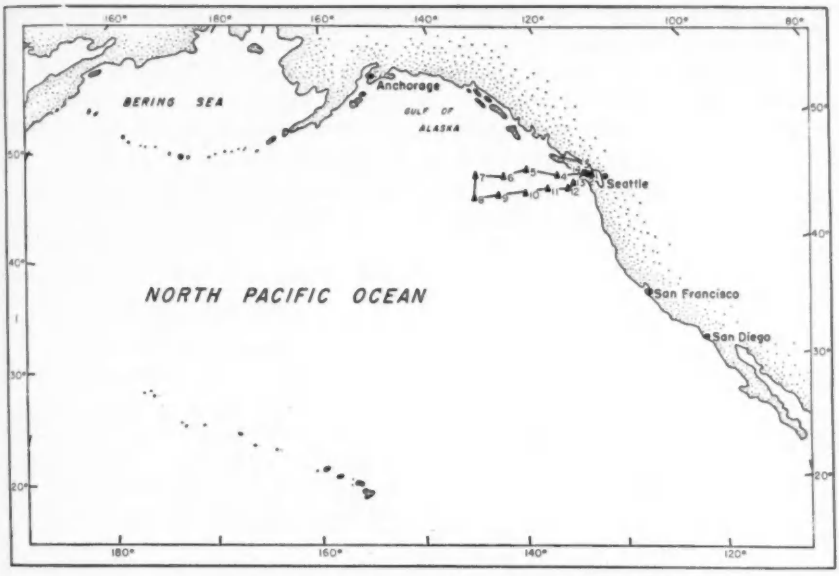

FIG. 1c. Cruise tracks showing hydrographic stations, *Brown Bear* Cruise 202.

A total of 574 hauls with the midwater trawls was taken during the three cruises: 452 of them with the 6-foot trawl and the remaining 122 with the 3-foot trawl. Of this total, 564 of the samples are considered in this report. The ten samples omitted from consideration were either lost at sea or were used for radio-isotope analysis.

METHODOLOGY

Samples were taken with 3- and 6-foot modified versions of the Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953). The cod-end in all nets was an 0.5-meter plankton net with a mesh opening of $\frac{1}{8}$-inch or 3.2 mm (Dupont Nylon, pattern 281, Marion Textiles, Inc., New York, N. Y.). It was fitted with a collecting bucket attached by means of a bayonet-type mount (Fig. 2).

Hauls were made at depths ranging from the surface to about 400 meters. At most hauls the net was fished 30 minutes at depth. The total time was measured from the time the net first entered the water until the haul was terminated and the net was removed from the water. All hauls were made with the ship proceeding with one engine under full speed, giving about 6.0 knots (11 km/hr). The net was released with the ship underway at towing speed, and was recovered with the ship's speed reduced to about 4.5 knots (8 km/hr). The hauls were made in a straight line along the cruise track.

The depth of fishing had been established by experiments prior to the cruises discussed in this report: a depth-distance recorder and a bathythermograph were attached to the cable just above the net; tows were made using different

lengths of cable and different towing speeds. Results of replicate hauls on three separate cruises showed the net to be consistently fishing at the same depth. The reliability of the results was further confirmed by intentionally hitting the bottom with the net and also by comparing the catches taken from above and below discontinuities of oceanographic variables which occurred at known depths.

Because of diurnal fluctuations in the availability of animals captured by the gear, the largest number of hauls was made during the night, with fewer hauls taken for comparative purposes during daylight. A standard series of hauls taken at depths of 30, 60, and 225 m was usually taken each night. Hauls taken at other depths, or repeat hauls at the standard depths, were also made to provide

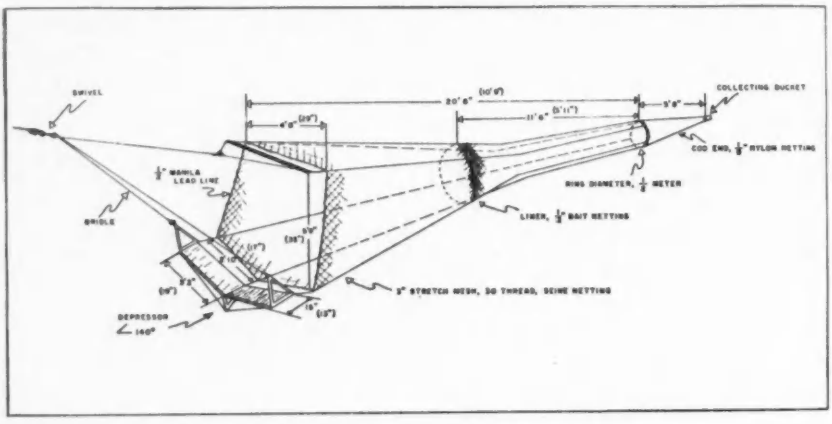

FIG. 2. Modified version of the Isaacs-Kidd midwater trawl.

additional information. Typically, six to eight samples were taken each night. Until new cable was supplied at San Diego during Cruise 199 the 225-meter depth represented the greatest sampling depth possible; the additional cable allowed sampling to a depth of about 400 meters.

The contents of each haul were preserved in 10% formalin and stored in 16-ounce screw-cap jars. Adult fish and other obvious nekton, such as squids longer than 75 mm and large shrimps, were removed from the samples in the laboratory. The settled volume was then determined by placing the sample in a 500-ml tapered graduate and allowing it to settle for at least 15 minutes. For the purposes of comparison these volumes were then divided by the total time of the haul in minutes; the resulting figure was recorded as the corrected plankton volume.

After completion of volume determinations, the hauls were examined and all fish larvae, molluscs, and annelids were sorted out. A representative sample (usually 5 to 10 animals) of each species of euphausiid, amphipod, copepod, pelagic shrimp, and mysid was removed from each haul. Samples of the less-frequently caught groups such as the coelenterates, crustacean larvae, isopods,

etc., were also removed. The dominant planktonic animal or animals for each haul were noted at this time.

Nearly all of the adult fish were identified to species; the larval fish were generally identified to family, although in some cases species identifications were made. The maximum and minimum total lengths for each species were recorded for each haul. The molluscs, other than cephalopods, were generally identified to species. Mysids were also identified to species. The above data for fish, molluscs and mysids are recorded in Aron, 1960. Studies of the remaining invertebrates have not been completed.

QUANTITATIVE EVALUATION OF THE MIDWATER TRAWLS

There are no satisfactory estimates of the volume of water filtered by the different sections of the net, nor are there any measurements of the catching power of the trawls in relation to other nets. This makes it difficult to compare trawl catches with catches by other standard plankton-sampling devices.

Maximum values for the filtering capacity of the trawl may be computed by multiplying the cross-sectional area of the mouth opening by the length of the water column through which the net passes. Table I, based upon a ship's

TABLE I. Quantitative evaluation of the midwater trawl. Ship's speed is taken as 6 knots.

	Section of the net					
	Front end (3-inch netting)		Middle section (3-inch netting, lined with ¼-inch bait netting)		Cod-end (1/8-inch netting)	
	6-foot	3-foot	6-foot	3-foot	6-foot	3-foot
Cross-sectional area of mouth opening, m^2	2.94	0.79	1.26	0.50	0.197	0.197
Water strained, m^3/min	544.00	146.00	233.00	92.50	36.400	36.400
Plankton concentration, g/m^3	0.006	...	0.13	...	0.083	...
Fish, g/m^3	0.002	...	0.005	...	0.030	...

speed of 6 knots, gives the maximum volume of water strained by different sections of the nets during one minute of trawling. Because the 3-foot net is not an exactly scaled-down version of the 6-foot trawl, the filtering capacities of the different sections are not proportional in the two nets.

The minimum amount of plankton and fish per cubic meter of sea water can be estimated by applying these values for filtering capacity. This minimum assumes: (a) that all water through which the net passes is filtered; (b) that each section of the net operates independently; and (c), that an animal is caught when it passes through the mouth opening of the particular section of the net.

For example: in the 78 oceanic night-hauls made with the 6-foot net in the upper 30 m, the average plankton catch was about 15 ml of plankton per minute towing. For these same hauls 1.5 fish were caught per minute of towing. Dividing the average plankton catch (based on settled volumes) by a factor of 5 (Redfield, 1941) the actual weight of plankton caught was about 3 g/min. The average weight of each fish caught was about 0.75 g. Using these weights and the assumptions made above, Table I shows the catch estimates made for each section of the 6-foot net.

Obviously the selectivity of the gear is different for each species. A euphausiid is more apt to pass through the 3-inch section of the net than through the section lined with the ½-inch bait netting. Once down in the cod-end, adult euphausiids are not likely to escape because of the small mesh. Fish once in the net are less likely to pass through the 3-inch netting than are the smaller invertebrates. Table II permits some estimate of the gross selectivity and escapement potential of the different groups by presenting data on the 15 pairs of hauls made with the two trawls. These pairs were made at night at depths of 30 and 60 m, with one haul of the pair immediately following the other as the ship maintained a straight-line course. The ratio of fish caught in the larger net to fish caught in the smaller net is 4.2 at 30 m and 3.7 at 60 m. The ratios of the plankton volumes are 3.1 and 2.9 in the 30- and 60-meter hauls. Larval fish ratios are 2.1 and 3.3 respectively in the 30- and 60-meter hauls.

The cross-sectional area, and hence the maximum filtering capacity, of the mouth opening of the 3-inch section of the 6-foot net is about 3.7 times more than the same section of the 3-foot net. Where the ½-inch bait-netting begins, the cross-sectional area of the large net is about 2.5 times that of the smaller trawl. The cross-sectional area of the cod-ends in the two different tralws is the same. The fact that the ratio of fish caught by the two nets closely approximates the ratio of the filtering capacity for the front section indicates that

TABLE II-a. Comparison of paired hauls made at 30 meters.

Six-foot net					Three-foot net				
	Haul No.	Plankton *ml/min*	Fish per haul	Larvae per haul	Haul No.	Plankton *ml/min*	Fish per haul	Larvae per haul	Cruise No.
	57	8.3	36	4	56	13.9	11	5	199
	67	42.1	109	7	66	10.7	34	8	199
	78	48.5	351	158	77	17.1	97	108	199
	84	62.1	108	128	83	8.1	18	34	199
	92	38.2	242	13	91	13.5	40	0	199
	37	0.7	0	90	36	0.1	0	31	202
	49	1.2	2	21	48	1.3	0	16	202
Total		201.1	849	421		64.7	200	202	
Average		28.7	121.3	60.1		9.2	28.5	28.9	
Ratio $\frac{\text{Catch of 6-foot net}}{\text{Catch of 3-foot net}}$						3.1	4.2	2.1	

TABLE II-b. Comparison of paired hauls made at 60 meters.

Six-foot net				Three-foot net				
Haul No.	Plankton *ml/min*	Fish per haul	Larvae per haul	Haul No.	Plankton *ml/min*	Fish per haul	Larvae per haul	Cruise No.
54	10.1	49	6	55	3.8	15	0	199
64	16.4	23	11	65	7.3	8	6	199
75	55.2	40	23	76	26.9	20	10	199
81	34.2	33	14	82	3.8	5	3	199
89	18.4	55	6	90	4.9	8	1	199
34	0.5	6	5	35	0.1	0	2	202
46	0.4	6	2	47	0.3	2	0	202
57	1.3	6	11	58	0.1	0	2	202
Total	136.5	218	78		47.2	58	24	
Average	17.1	27.3	9.8		5.9	7.3	3.0	
Ratio $\frac{\text{Catch of 6-foot net}}{\text{Catch of 3-foot net}}$					2.9	3.7	3.3	

escapement through the 3-inch mesh is probably negligible for fish. As expected, the plankton-catch ratio (approximately 3) indicates that some escapement occurs through the 3-inch netting but that the front section serves to trap at least part of the plankton. The ratio for the larval-fish-catch is a little less than the plankton-catch ratio, indicating a still greater escapement through the coarse mesh. As the larval fish are smaller on the average than most of the plankton caught by the trawls their higher escapement through the 3-inch section of the net can be expected. The estimate of 0.002 gram of fish per cubic meter of sea water is probably a realistic value. Because of escapement, however, the value for the weight of plankton probably lies between 0.005 and 0.013 g/m^3.

The plankton concentrations referred to here are for plankton populations a step higher on the food chain than those caught in gear such as the Clarke-Bumpus net or the standard 0.5-meter plankton nets. This is verified by the fact that the estimate made for the weight of fish per cubic meter of water is not much less than the estimate of the plankton. The bulk of the fish taken were myctophids; the most abundant plankton were euphausiids, large copepods (*Calanus cristatus*), and the pelagic shrimp (*Sergestes spp.*). Except for the shrimp, all of these form important items in the diet of the Pacific salmon (Allen and Aron, 1957; Andrievskaya, 1958), additional evidence of their similar positions in the food chain.

CONSISTENCY OF SAMPLING

It is essential to demonstrate that qualitative and quantitative variations encountered during a study are not the result of the sampling process. Variations due to sampling are inevitable in any biological study and these must be kept

smaller than the actual variations being studied to give significance to the results.[4] Variations encountered under relatively uniform oceanographic conditions are considered in this section and it is shown that these are insignificant when compared to those variations found to occur between different oceanic regimes.

Pairs of hauls[5] made with the 6-foot net during the same night at a depth of 225 m are compared in terms of volume of plankton and numbers of fish caught. The paired hauls, made on Cruise 199, are: 34, 37; 63, 68; 80, 85; 88, 93; 96, 97; 104, 107; 112, 113; 122, 127; 131, 136; 149, 153; 169, 175; and 241, 242 (Fig. 3). Examination of the catches showed that the species composition, particularly in regard to the dominant animals, is very much alike in the paired hauls. The second haul of the pair, however, generally catches more species. The additional species are almost always represented by a few specimens of stomiatoid fishes which probably reside at greater daytime depths than the more abundant species caught by the trawl. The first haul probably was taken at a time before the species completed their vertical migration, but they were available to the trawl by the time the second haul was made.

Figure 3 shows that the difference in volume and number of fish caught between each of the paired hauls is always less than a factor of two. Although none of the samples was taken from exactly the same section of open ocean, conditions at a depth of 225 m are relatively uniform over the distance involved in making a pair of hauls.

Quantitative and qualitative variations are much greater in areas that present different physical and chemical conditions. Table III compares the average catches of night hauls on Cruise 199 made at three depths from Stations

TABLE III. Catches made in areas between Stations 3 and 10, and Stations 21 and 30, Cruise 199.

Station and Area	Depth (*m*)	No. of hauls	Plankton (*ml-min*)	No. of fish	Average number of myctophids taken per haul			
					L. leucopsarus	*D. theta*	*C. townsendi*	*L. ritteri*
3–10	20–30	8	28.6	128.5	93.5	19.4	0.0	0.0
21–30	20–30	11	0.9	13.0	0.0	0.2	4.9	2.1
3–10	31–60	11	22.1	43.1	26.3	5.1	0.0	0.8
21–30	31–60	9	1.0	26.7	0.0	0.3	5.9	9.0
3–10	121–250	11	7.8	25.9	12.5	2.5	0.0	1.5
21–30	121–250	10	1.7	20.1	0.0	0.2	1.1	3.8

3–10, an area dominated by Subarctic water, and Stations 21–30, an area characterized by the influence of Intermediate, Central, and Equatorial water together with the presence of Subarctic water. More than 20 times as much plankton is caught in the upper 60 m in the northern hauls, and even in the hauls made at greater depths the northern catches are more than 4 times larger than those

[4]The sampling problem resulting from the highly non-uniform distribution of animals is discussed in a following section dealing with plankton patchiness.

[5]Locations of hauls and stations referred to throughout this discussion are shown on Fig. 8.

made in the south. Except for the hauls taken in the upper 30 m where the northern catches are considerably greater than those to the south, the numbers of fish caught at the different depths are much alike. These catches, however, show the northern hauls to be dominated by *Lampanyctus leucopsarus* and *Diaphus theta*, and the southern catches to be dominated by *L. ritteri* and *Ceratoscopelus townsendi*. The distribution of these species is almost mutually exclusive and there is only a slight overlap in their ranges.

From these data it appears that variations imposed by sampling procedure are of minor importance in the interpretation of the data.

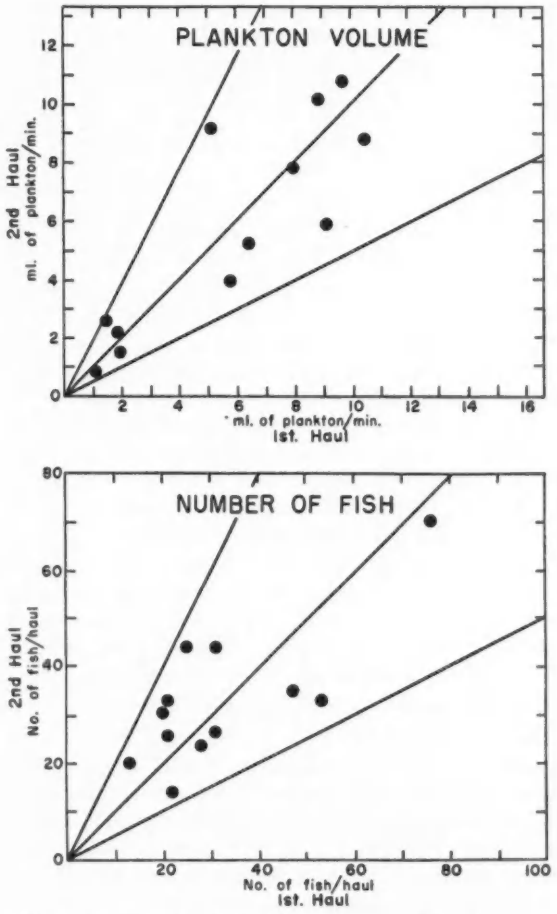

FIG. 3. Comparison of plankton and fish catches of paired hauls taken at a depth of 225 meters.

VARIABILITY IN PLANKTON ABUNDANCE

Plankton Patchiness

Plankton patchiness may be defined as non-uniform distribution of plankton populations resulting in dense swarms or patches within a small area. Aron (1958) has discussed some of the implications of patchiness with regard to sampling the smaller plankton caught in a 0.5-meter net and by a plankton pump. In the present study the nature of the gear and the method of towing miminizes the effects of patchiness; however, definite evidence of swarming is still apparent in the catch from several of the tows.

The most obvious case of patchiness is seen in the catches from Hauls 59 and 60 of Cruise 202. Both hauls are taken at a depth of 30 m, one haul immediately following the other. The first haul was taken with the 3-foot trawl and produced a catch of 25.7 ml of plankton per minute of trawling. The second haul was taken with the 6-foot net and caught only 0.4 ml/min. The larger catch was made up almost exclusively of sergestid shrimps. The smaller catch consisted of amphipods and euphausiids, and was very similar to other hauls made at the same depth in about the same area, but the catch of sergestids was larger than the catch made in any haul, regardless of depth, between Stations 10 and 12. Another example of the same phenomenon can be seen in Hauls 46 and 48 of Cruise 199. There was a 49-minute time gap between the completion of the first haul made with the 6-foot net and the beginning of the second haul, using the 3-foot net. The first catch consisted of a mixture of euphausiids and sergestids and had a settled volume of 7.2 ml of plankton per minute of trawling. The catch made with the smaller net consisted almost entirely of sergestids and had a volume of 100.0 ml/min. Here again the very large catch cannot be considered as typical of the area for, with the exception of inshore hauls, it is the largest catch made during any of the three cruises, in spite of the fact that the smaller net was used. Further instances of patchiness were encountered in hauls made with the same net towed at similar depths at relatively close time intervals. On Cruise 202, Hauls 41 and 44 were both made at the surface using the 6-foot net; the first caught 33.9 ml of plankton per minute, the second only 3.6 ml/min. Hauls 43 and 49 of Cruise 202 caught 25.7 and 1.2 ml/min; both of these hauls were made with the 6-foot net at 30 meters. In all of the cases just cited, sergestids were found almost to the exclusion of all other animals in the large catches; in fact, wherever patchiness occurred during these cruises, it was the sergestid shrimp which was the dominant animal.

The cause of patchiness is not thoroughly understood. Patchiness may be associated with the behavior patterns of the animals or it may be a direct function of a kind of oceanographic patchiness, the occurrence of islands of one type of water within another. In the case of the sergestids, schooling movement certainly seems possible for, according to Welsh and Chase (1938), "... the last two pairs of thoracic legs are flattened and shorter than the other three pairs and fringed with long hairs. These, in conjunction with the long well developed pleopods suggest that the sergestids are among the fastest swimming of the

pelagic Crustacea." The fact that virtually all of the cases of patchiness occurred in areas around transition zones between different water masses gives strength to the possibility that the swarming is conditioned by physical-chemical factors.

Seasonal and Year-to-Year Variation

On land it is possible to select a particular geographic location and then study, with a reasonable degree of precision, the seasonal and year-to-year changes of the flora and fauna that inhabit the area. This is not possible in studying pelagic organisms because their substratum is not fixed in any one position but meanders in a more or less unpredictable fashion. Studies made at a fixed geographic location are not necessarily time-studies of a specific population but may actually represent short glimpses of very different, and in some cases only distantly related, populations that are residents of a particular water mass.

Water-mass movement is relatively slow; hauls taken within two months of one another at about the same geographic point are likely to be taken in the same water mass unless the region in which the hauls were taken is at a boundary between two water masses.

During Cruises 176 and 199 the cruise track crossed so that hauls were taken at about a one-month interval in approximately the same location. Table IV presents data from hauls taken in these areas. Unfortunately, the data

Table IV. Hauls taken between Stations 16 and 17 and Stations 27 and 28, Cruise 199.

Station Nos.	Depth (*m*)	Plankton (*ml/min*)	Fish per haul	Species per haul	Larvae per haul
16–17	30	2.3	49	8	2
27–28	30	3.5	27	4	5
16–17	60	6.8	47	6	4
27–28	60	2.0	22	5	2
16–17	120	6.5	21	8	3
27–28	120	8.9	22	7	4
16–17	225	2.9	29	11	4
27–28	225	3.1	26	9	5
Hauls	Data Taken from Hauls 23 and 104, Cruise 176				
23	225	2.1	6	1	1
104	225	2.2	2	1	2

for Cruise 176 from the area where the cruise track crossed is represented by only two hauls taken during the day at a depth of 225 meters. Hauls taken just west and south of the crossing on this cruise are not strictly comparable because of diurnal effects, and the hauls to the south of the crossing are probably affected by the Subarctic Current. The data from Cruise 199 were taken from between Stations 15 and 16 and between Stations 27 and 28, for physical and chemical

conditions in these areas are similar. The species composition of these hauls is much alike, particularly in regard to the dominant species. These data show that variations encountered on a monthly scale are in the range encountered in hauls made during the same night. These variations, however, are small when compared to the differences between water masses, which will be shown to be as much as 100-fold in terms of volume of plankton and nearly mutually exclusive in terms of species composition.

On a year-to-year basis, however, physical and chemical variations at a particular point may be extensive. Tully *et al.* (1960), for example, have shown extensive changes in waters off the Pacific Coast of Canada during the 4 years beginning with 1955. Such variations make it necessary to consider a particular water mass rather than a fixed geographic location when studying the year-to-year changes of pelagic populations. Table V presents data based upon hauls

TABLE V. Year-to-year variations of animal abundance. (Cruise 176, 1957; Cruise 199, 1958)

Cruise No.	Depth (*m*)	Plankton (*ml/min*)	Fish per haul	Species per haul	Larvae per haul	*Lampanyctus leucopsarus* per haul
176	20–30	43.7	67.9	2.8	43.4	55.7
199	20–30	28.6	128.5	5.9	46.1	93.5
176	31–60	12.7	21.2	2.4	7.8	17.9
199	31–60	22.1	43.1	5.2	10.0	26.3
176	121–250	5.8	14.5	4.1	5.3	6.3
199	121–250	7.8	25.9	6.0	15.4	12.5

made with the 6-foot net taken in the Subarctic water of the Gulf of Alaska. These data include all of the night hauls taken between Hauls 4 to 37 and 89 to 123 of Cruise 176 and all of the night hauls taken between Stations 3 and 10 on Cruise 199. These data were selected for comparison because, although the geographic areas sampled in the two years are different, physical and chemical conditions in the two areas are similar.

Table V shows that the year-to-year differences are generally small, usually within a factor of 2 and never exceeding a factor of 3. The lower average number of species caught per haul on Cruise 176, however, does seem significant. The higher number of species caught per haul on Cruise 199 may be influenced by the occurrence of southern forms displaced to the north by the intrusion of Intermediate water. These species, however, made up only a small portion of the catch, for *Lampanyctus leucopsarus*, the fish caught most frequently during the studies, dominated the fish catch and occurred in about the same abundance on each of the two cruises.

VERTICAL MIGRATIONS

The vertical migrations of many planktonic organisms are well known, particularly those which are diurnal in nature. The early literature is reviewed in detail by Russell (1927) and the more recent literature is covered by Cushing

(1951). Nearly all of the latest studies of vertical migration concern the Deep Scattering Layer (DSL) and related phenomena; this literature is summarized by Soli (1959).

The DSL observations point to concentrations of animals residing at a depth of about 300 to 800 m during the daylight hours and migrating close to the surface at night. That this diurnal migration is influenced by light is well documented by such work as that of Clarke (1933, 1936) and Clarke and Backus (1956), and especially that of Bogorov (1946) who shows that species which undergo diurnal vertical migrations where there are day-night conditions do not migrate in the Arctic when no day-night conditions exist.

To eliminate the influence of diurnal fluctuations from the analysis, hauls taken in daylight hours were separated from those taken at night. Hauls taken between 1 hour after sunset and 1 hour before sunrise were considered night hauls; hauls taken at other times were considered day hauls. Table VI summarizes data obtained using the 6-foot net and, with the exception of hauls

TABLE VI. Diurnal variations of animal abundance, from data obtained in off shore hauls with the 6-foot net.

	20–30 *m*		31–60 *m*		61–120 *m*		121–250 *m*		251–400 *m*	
	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day
Number of hauls	78	30	67	33	29	6	88	42	21	6
Average plankton volume ml/min	14.7	0.4	12.2	1.9	10.8	2.0	6.3	3.3	4.8	0.9
Average no. of fish per haul	54.5	1.7	33.6	1.3	17.1	2.2	24.0	5.4	33.7	6.8
Average no. of larvae per haul	28.3	5.7	17.6	4.5	10.6	2.3	9.0	4.1	11.6	5.0
Average no. of species per haul	3.3	1.0	4.4	0.5	5.1	1.0	6.5	1.0	8.2	2.7

made in the Aleutian region, only includes offshore hauls made between hydrographic stations. These data show that in the night hauls the volume of plankton diminished with depth, and the number of fish species caught per haul increased with depth. The number of fish and fish larvae also decreased with depth until the deeper hauls in which the trend is reversed. The increased numbers are made up of mostly gonostomids and other stomiatoid fishes which also contribute to the species increase in the deeper waters. These species may be part of the two deep scattering layers noted by Batzler and Westerfield (1953) at about 400 and 700 m which, according to the authors, do not participate in the diurnal migration. This latter theory may be questionable since no observations were made on these deeper layers during daylight hours, their possible occurrence being obscured by the main scattering layer. This leaves the possibility that animals making up the deeper layers may migrate still deeper during daylight hours. A suggestion that this really occurs is indicated by the day

hauls showing a regular increase in plankton volume with depth, until the deepest hauls where there was a sudden decrease. The number of fish and fish species, however, increased with depth even to the deepest hauls made. Further complications are added by the distribution of larval fish, which during the daylight hours maintain the same pattern of vertical distribution as during the hours of darkness. Regardless of depth, the night hauls caught a substantially greater biomass than the day hauls. The cause of this differential is uncertain, but it is most likely that during the day animals migrated to depths outside the range of the available equipment. Other possible causes of this differential include better escapement potential of the animals in the daytime, and greater scatter during the daylight hours.

Diurnal migrations are also influenced by local physical and chemical conditions. Weston (1958) showed a definite scattering layer at the thermocline in the North Sea. Hansen (1951) showed that different species, mostly of copepods, had a differential reaction to the thermocline: some preferred residence above the discontinuity layer, some below, some within the layer, and some species remained little affected. Other modifying influences, including weather, sunlight, phytoplankton distribution, and the age of the migrating plankton are discussed by Cushing (1951).

The surveys revealed diurnal migration of plankton to be modified by physical and chemical regimes. Figure 4 shows vertical temperature distributions observed during Cruise 176. The first section is typical of the northern,

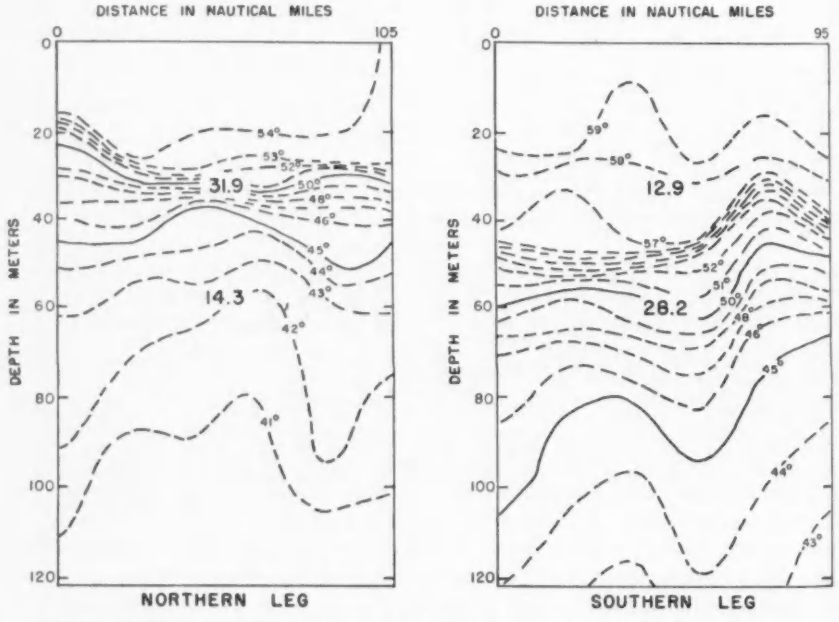

FIG. 4. Vertical temperature profiles from northern and southern legs of Cruise 176.

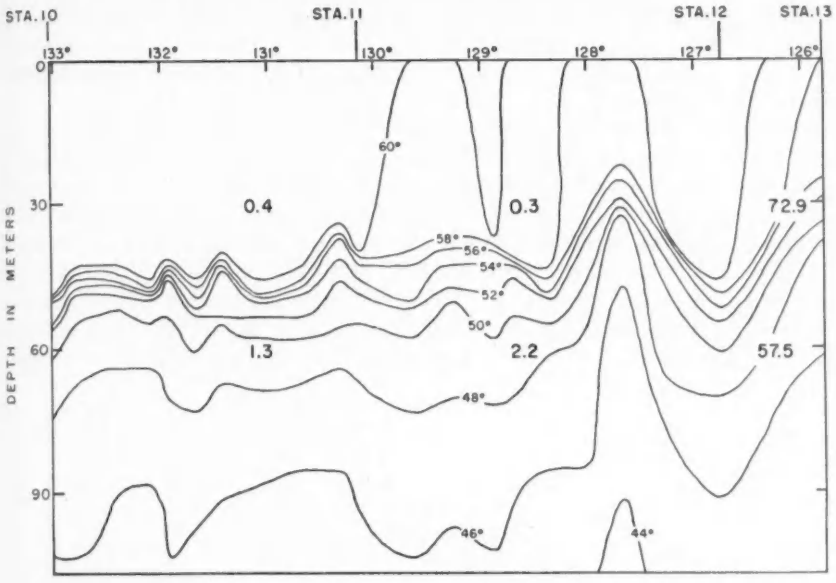

FIG. 5. Vertical temperature profile between Stations 10 and 13, Cruise 202.

outward leg of the cruise. Plotted on this section are the average catch data for the hauls made with the 6-foot net at depths of 30 and 60 m. These averages include all of the 30- and 60-meter hauls taken at night between Haul 4 and Haul 30. The second section is a typical segment taken from the southern, inward leg and also includes the average catch data for the hauls made at 30 and 60 m; these data include all 30- and 60-meter night hauls made between Hauls 124 and 148. For the northern leg of the cruise a greater catch was made at 30 m than at 60 m; the reverse was true for the southern portion. Temperatures and the depth of the thermocline for the two legs were different: the 50°F (10°C) isotherm occurred at about 30 m in the north and at 60 m in the south; also, the thermocline was deeper in the south so that hauls made on the southern leg at a depth of 30 m were taken above the thermocline.

The same type of modification is found in data obtained during the third of the survey cruises: Figure 5 shows a vertical temperature distribution obtained during Cruise 202 between Stations 10 and 13. Plankton volumes for hauls made with the 6-foot net at 30 and 60 m are plotted on this section. For hauls between Stations 10 and 12 the catch at 30 m (above the thermocline) was far lower than the catch at 60 m (below the thermocline). Between Stations 12 and 13, colder water was closer to the surface, and the catch for the haul made at 30 m was greater than the catch for the 60-meter haul. Besides showing a change in the vertical distribution of animal abundance, the catches made between Stations 12 and 13 showed very much greater quantity than catches made further to the west. Part of this increase is undoubtedly due to the proximity to land and

the influence of the Strait of Juan de Fuca. Part of the apparent increase, however, seems to be the result of a second kind of modification of the vertical migration pattern, in effect reducing the animal abundance in the upper waters west of Station 12.

Figure 6 presents temperature-salinity diagrams constructed from data obtained at Station 8 (Cruise 199) and Stations 6 and 10 (Cruise 202). Average catch data obtained in the hauls made with the 6-foot net in each of the areas are shown in Table VII. The averages are based on night hauls and include all hauls made between Stations 7 and 9 (Cruise 199) and between Stations 5 through 7 and 8 through 11 (Cruise 202), with the exception of two hauls, 20 and 43 (Cruise 202), which are eliminated from consideration because the author believes them to be unrepresentative for reasons discussed in the section dealing with plankton patchiness. All of the T-S diagrams show the typical quasi-isothermal

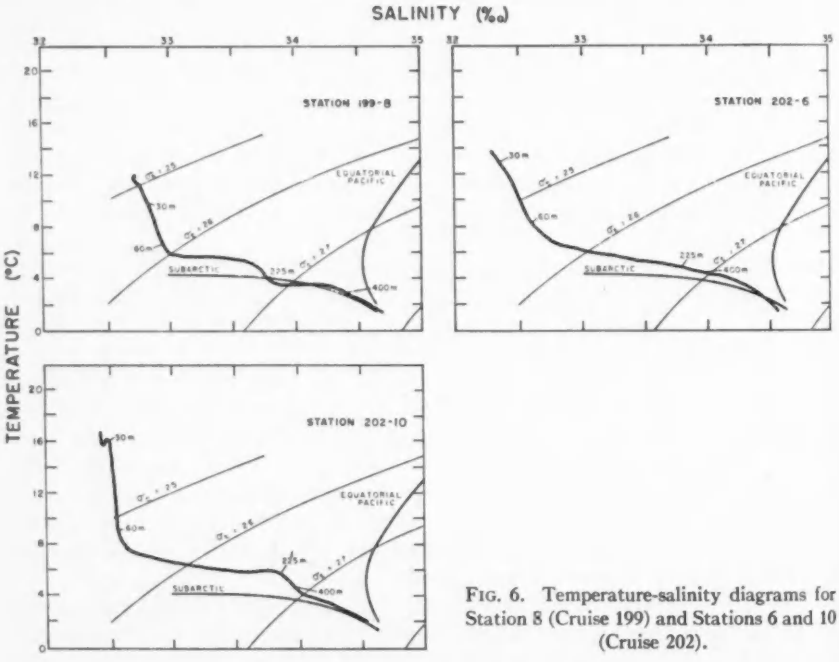

FIG. 6. Temperature-salinity diagrams for Station 8 (Cruise 199) and Stations 6 and 10 (Cruise 202).

halocline discussed by Fleming (1958b), but several differences between the diagrams are apparent. The curve for Cruise 199 is fairly typical of Subarctic conditions: the top of the halocline is at a depth between 75 and 100 m; the temperature at the top of the halocline is about 6.0°C; and all temperatures within the halocline are under 6.0°C. The T-S diagram from Station 10 of Cruise 202, although showing the presence of considerable Subarctic water, shows the intrusion of Intermediate water at a depth between 200 and 400 m. The top of the halocline is still between 75 and 100 m; however, the temperature at the

top is 8.0°C and all temperatures within the halocline are greater than 6.0°C. The T-S diagram for Station 6 presents an almost intermediate condition between the other two curves.

TABLE VII. Variation of plankton volume and numbers with depth in certain sections of Cruises 199 and 202.

Cruise No.	Station and Area	Depth	Plankton	*L. leucopsarus*		*D. theta*	
				No. per haul	Frequency	No. per haul	Frequency
		m	*ml/min*				
199	7–9	20–30	55.3	198.0	2/2	12.0	2/2
202	5–7	20–30	3.2	3.0	2/2	0.0	0/2
202	8–11	20–30	1.4	0.0	0/4	0.0	0/4
199	7–9	31–60	35.5	37.7	3/3	3.0	2/3
202	5–7	31–60	13.6	20.0	3/3	14.0	3/3
202	8–11	31–60	0.7	1.0	2/3	0.3	1/3
199	7–9	61–120	No hauls at this depth				
202	5–7	61–120	5.3	1.0	1/1	3.0	1/1
202	8–11	61–120	7.3	1.3	2/3	3.7	3/3
199	7–9	121–250	9.4	11.7	3/3	1.3	2/3
202	5–7	121–250	9.5	0.5	1/2	0.5	1/2
202	8–11	121–250	8.2	1.3	2/3	1.0	2/3
199	7–9	251–400	No hauls at this depth				
202	5–7	251–400	4.6	21.0	2/2	1.5	2/2
202	8–11	251–400	5.3	1.7	3/3	0.7	2/3

In the area influenced by the intrusion of Intermediate water neither the plankton nor *Lampanyctus leucopsarus* and *Diaphus theta* (the two most common fishes taken during the surveys) are capable of significant penetration through the halocline. Some differences in the species composition of the plankton are also apparent. The catches from the Subarctic waters are dominated by the copepod *Calanus cristatus* and by arrow worms, *Sagitta spp.*, animals much less significant in catches made in the area characterized by the intrusion of Intermediate water. In the environment influenced by the Intermediate waters pelagic shrimp of the genus *Sergestes*, however, are of greater importance than in the more strictly Subarctic regime. Midway between the two extremes, migration through the halocline occurs although there was no significant penetration through the thermocline by either fish or plankton.

Temperature inversions appear to affect the migration patterns of the plankton. Figure 7 presents a vertical temperature section made between Stations 11 and 12 (Cruise 199), and shows a temperature inversion between about 100 and 200 m; the volume of the plankton catch according to depth is also shown. Both above and below the inversion the catch was low (1.1, 2.4, and 6.0 ml/min of trawling at 30, 60 and 225 m) but it was high within the inversion (17.3 and 20.4 ml/min at 120 and 160 m).

Diurnal migrations may be impossible in areas of extensive mixing because of water too turbulent for the swimming abilities of the animals involved. For

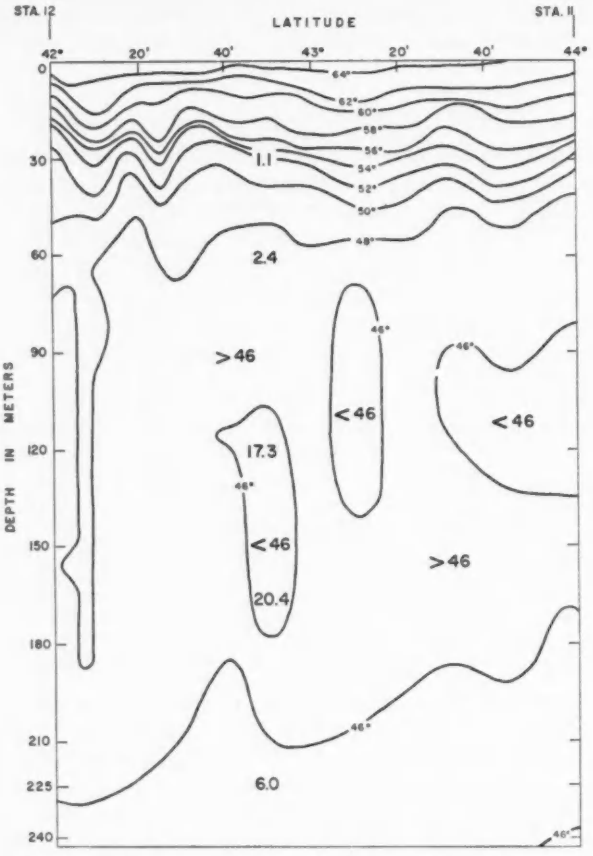

FIG. 7. Vertical temperature profile between Stations 11 and 12, Cruise 199.

the area considered in this study, such a turbulence occurs only in the Aleutian passes, but insufficient data from the surveys are available to demonstrate such a deviation. However, the author found no diurnal fluctuations during a 24-hour survey of the Colvos Passage-Tacoma Narrows region of Puget Sound (a region of high current velocities and virtually top-to-bottom mixing). The average volumes were 0.5 ml/min both for 12 day-hauls and for 9 night-hauls, and the highest and lowest catches for both day and night were also identical.

The above examples are not intended to show that temperature and salinity are the effective barriers to diurnal migration. Temperature and salinity serve only as convenient and available measures of physical and chemical conditions which, from the biological point of view, are still poorly understood. Under usual conditions, an animal migrating from 400 m to the surface must pass

through greater temperature and salinity changes than occur in the thermocline, halocline, or inversions. The steepness of the gradient might be the effective barrier, but the mechanics of the barrier cannot be explained with our present knowledge of the physiology and behavior of the plankton and pelagic fishes.

RELATIONSHIP OF PHYSICAL AND CHEMICAL CONDITIONS TO THE DISTRIBUTION OF ANIMALS

The distribution of marine animals in relation to physical and chemical conditions has been the subject of much study. Russell's work in the North Sea, summarized in his 1939 paper, stimulated the study of "plankton indicators", so that there is an overwhelming number of publications on chaetognaths in the bibliography of the field. Such papers as those by Sund and Renner (1959) and by Bieri (1959) clearly show their dependence upon the approach developed by Russell.

In most of the studies of organisms which might have significance as indicators of physical and chemical conditions, the species used are not readily identifiable in the field. In the case of diatom studies (Graham and Bronikovsky, 1944; Marumo, 1957), the species are microscopic and shipboard identification is impossible except under very special conditions. In the case of macroscopic plankton, chaetognaths (Bieri, 1959), euphausiids (Boden *et al.*, 1955), some pteropods (Hida, 1957; Tesch, 1946, 1948), and the copepods (Johnson, 1956; Mednikov, 1958), identification can only be made by well-trained personnel and in most instances positive identification requires shore-based microscopic examination.

It has been nearly impossible to use larger animals as indicators until recently, when the development of the Isaacs-Kidd midwater trawl provided a convenient device for sampling the macroplankton and smaller nekton. Several species of fish and pteropods, all easily identifiable in the field, have distributions which are closely related to the distribution of water masses. The distributions of these and other forms and also the variations in standing crop of macroplankton, will be considered in relation to the physical and chemical conditions of the sampling area. The terminology used for water masses and currents considered will generally be that of Sverdrup *et al.* (1942).

Figure 8 presents data showing the relative standing crop of macroplankton in the Eastern North Pacific. These data are presented as the volume of plankton in milliliters per minute of trawling; they represent the average catch of a series of night hauls made at depths of 30, 60, and 225 meters with the 6-foot net, except for the area between Stations 33 and 38 of Cruise 199 when data obtained from the 3-foot trawl are used. Hauls taken at 400 m are not considered in these averages for no data from this depth are available from the 1957 survey.

Data obtained in 1957 show a decreasing abundance of plankton with an increasing distance from the coast. The plankton volume decreases from 33.9 ml/min just off the Washington Coast to 5.0 ml/min south of Kodiak Island. Just south of the Alaska Peninsula, adjacent to an area of low catch, the volume

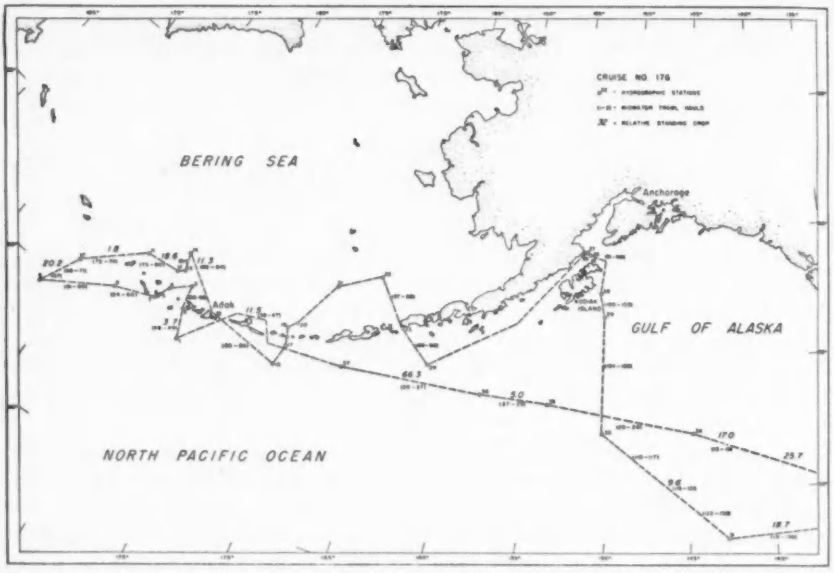

FIG. 8a. Cruise tracks showing position of hydrographic stations, position of hauls and relative standing crop of plankton, *Brown Bear* Cruise 176.

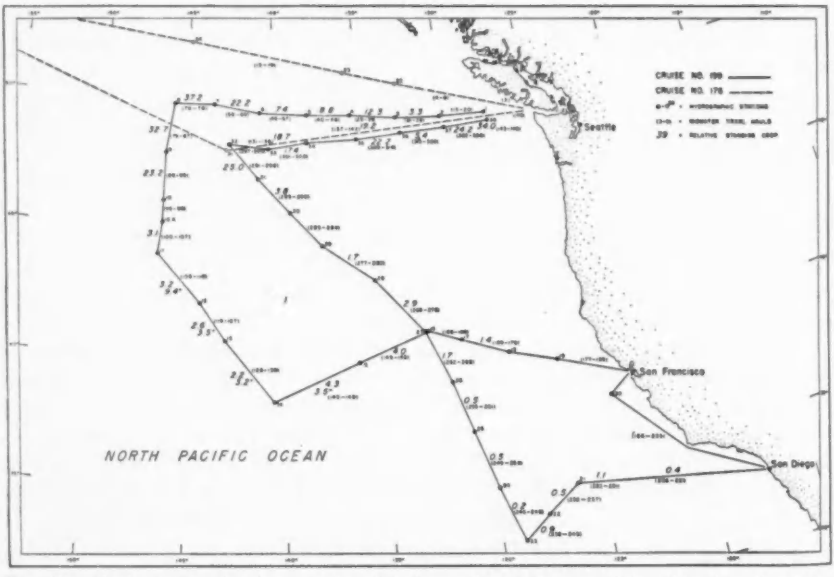

FIG. 8b. Cruise tracks showing position of hydrographic stations, position of hauls and relative standing crop of plankton, *Brown Bear* Cruise 199. Figures with an asterisk (*) are values which include hauls taken within the temperature inversion.

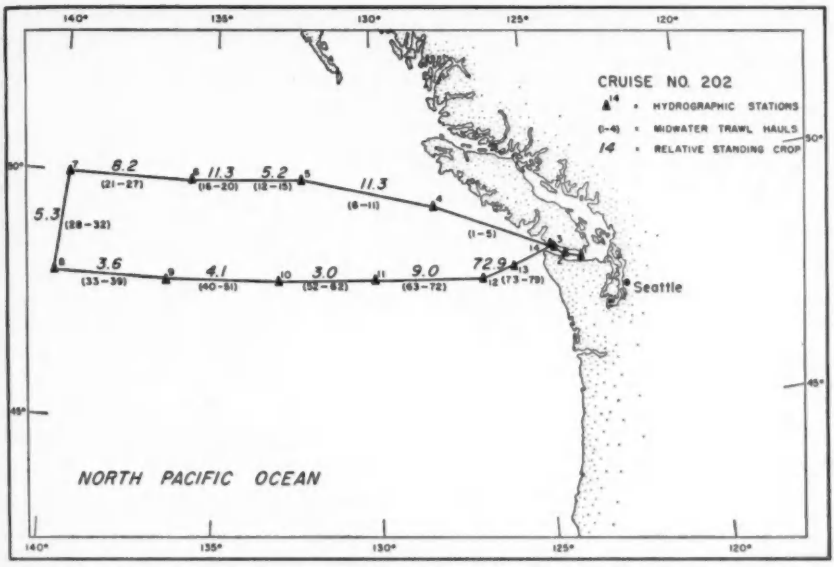

FIG. 8c. Cruise tracks showing position of hydrographic stations, position of hauls and relative standing crop of plankton, *Brown Bear* Cruise 202.

increases sharply to 66.3 ml/min. This increase takes place at a transition between two oceanographic areas which Fleming (1955) terms the Alaskan Coastal Region and the Alaskan Gyral. These areas are separated by the strong southwestward-flowing current of the Alaskan Stream (Bennett, 1959). Oceanographic data from the area of high plankton abundance show higher concentrations of phosphates and lower amounts of oxygen than from the area of lower abundance more central to the Gulf of Alaska.

In the Aleutian Islands the plankton catch is variable; within short geographic distances the volume of plankton caught may change by a factor of 10. For example, Hauls 75-77 have an average volume of 1.8 ml/min. These hauls were taken between two other series (Hauls 68-70 and 78-80) having average volumes of 20.2 ml/min and 18.6 ml/min. Figure 9 shows vertical temperature sections of the area in which these series were made. The large catches, dominated by euphausiids, were made in areas of high stability while the low catch, consisting mostly of copepods and chaetognaths, was made in an area of neutral stability. Hauls 50, 51, and 52, which resulted in an average volume of 3.7 ml/min composed mostly of copepods and chaetognaths, were also taken in an area of neutral stability.

Areas that are intermediate in their vertical temperature distribution are also intermediate with respect to their biota. Hauls 82-84 have an average volume of 11.3 ml/min, which is between the high and the low values for the Aleutian area. In Haul 81, with a corrected plankton volume of 1.3 ml/min, copepods and euphausiids have about equal quantitative importance.

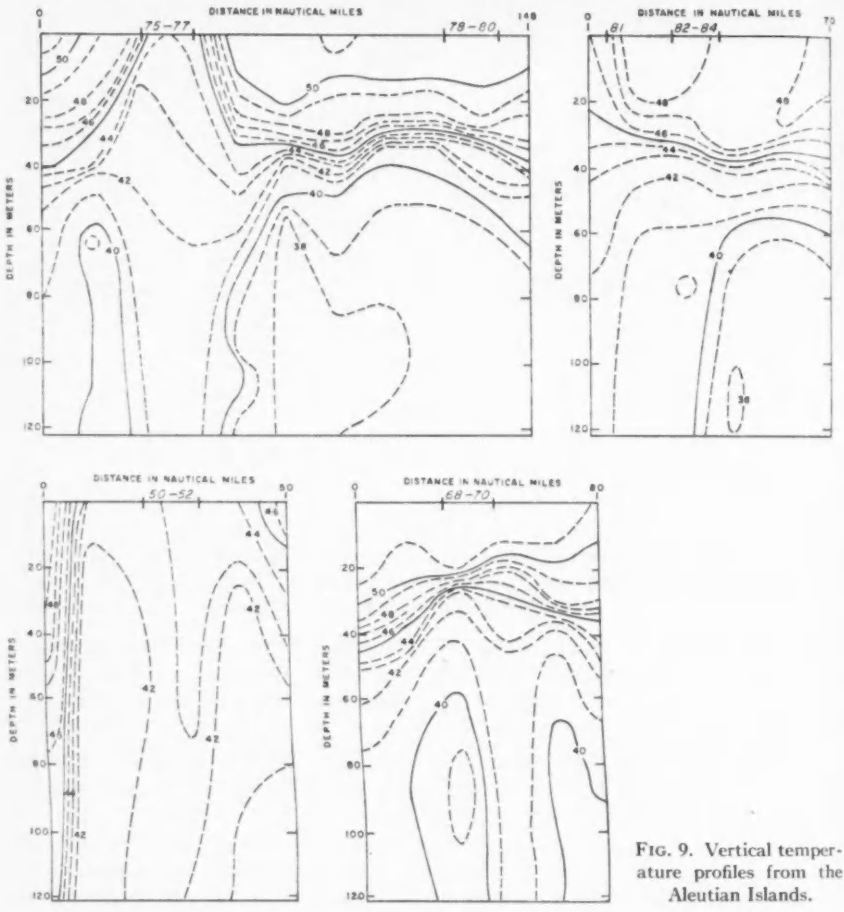

FIG. 9. Vertical temperature profiles from the Aleutian Islands.

The low standing crop in areas of either neutral stability or high turbulence may be a real index of low productivity. The results shown above for the zooplankton closely agree with results obtained in phytoplankton work by Gran and Braarud (1935), Riley (1942), and Sverdrup (1953). These workers all demonstrated that where the surface mixed layer was deep the productivity was low despite high nutrient concentrations. If phytoplankton production has a low average rate, the establishment of large populations of grazing animals is obviously impossible.

The average volumes of hauls taken on the northern and southern legs off the Strait of Juan de Fuca are similar. The vertical distribution of the catches (discussed in the section dealing with vertical migration) is different. Displacement of the maximum catch from the 30-meter hauls on the northern leg to the

60-meter hauls on the southern leg appears to be the result of the influence of the Subarctic Current. The surface waters in the area influenced by the Subarctic Current are both warmer (by as much as 4.0°C) and more saline (by as much as 0.20‰) than waters not influenced by the Subarctic Current. A number of fish species, previously unencountered to the north, were found on the southern leg. These will be discussed in a following section.

The 1958 collections, because of their wider latitudinal coverage, included a greater variety of physical and chemical conditions than the collections made in 1957. The differences in environments are paralleled by changes in the biota. Comparison of the standing crop estimates based upon the 1958 surveys with the estimates made in 1957 reveal some of the influences exerted in a particular geographic locale by physical and chemical conditions.

In 1958 the largest standing crop occurred in the sampling area furthest to the west, unlike the standing crop in 1957 when the catch decreased with an increasing distance from the Strait of Juan de Fuca. Between Stations 2 and 3 of Cruise 199 the plankton catch is only one-tenth that of 1957 in about the same geographic area. Low catches of 5.4 ml/min and 5.2 ml/min were also recorded in the same general area on the homeward leg of Cruise 199 and between Stations 5 and 6 of Cruise 202[6].

On all of the East-West cruise legs made between 46° and 53°N standing crop estimates are about the same, except for the southernmost leg (the homeward leg of Cruise 202) and the 3 haul series mentioned in the previous paragraph. Catches made on the southernmost leg are low except close to shore. The T-S diagrams from these areas show a number of differences which parallel the biological variations. Figure 10 shows the T-S diagrams from Station 32 of Cruise 176; Stations 2, 3, and 36 of Cruise 199; and Stations 5 and 6 of Cruise 202. (T-S diagram for Station 10, Cruise 202, is shown in Fig. 6). High plankton catches were associated with conditions demonstrated by the T-S diagrams from Station 32 of Cruise 176, Station 3 of Cruise 199, and Station 6 of Cruise 202. Low plankton catches were associated with conditions shown by the T-S diagrams from Stations 2 and 36 (Cruise 199) and 5 and 10 (Cruise 202). Differences are apparent between the T-S diagrams from rich areas and those from areas of low plankton abundance. Low catches were made in areas characterized by an extensive intrusion of Intermediate water into the predominant Subarctic water: temperatures within the halocline were mostly above 6.0°C; at the top of the halocline the temperature exceeded 8.0°C; and the surface temperature exceeded 15°C. High catches were taken in areas where the influence of Intermediate water is either absent or much less significant: temperatures within the halocline, except at Station 32 (Cruise 176), were mostly below 6.0°C; at the top of the halocline the temperature was less than 8.0°C, and the surface temperatures were below 15°C. Comparisons are particularly striking between the T-S diagrams

[6]Mechanical difficulties with the main winch prevented the use of the 6-foot trawl during the last stages of Cruise 199. Because of the winch problems, all hauls taken between Stations 33 and 38 were made with the 3-foot trawl. The average plankton volumes obtained from these hauls are multiplied by 3, a factor based upon a series of paired hauls using the 3-foot and 6-foot nets. These hauls will be discussed under the section dealing with the quantitative evaluation of the trawls.

at adjoining stations, those made at Stations 2 and 3 (Cruise 199) and at Stations 5 and 6 (Cruise 202). The physical and chemical differences are obvious and the short time-interval between the haul series removes the possibility of results being distorted by seasonal or yearly changes. Figure 6 (T-S diagram from Station 8 of Cruise 199) shows that in this area the intrusion of Intermediate water was slight, the halocline temperatures were all below 6.0°C, and the surface temperature was below 12.0°C. This T-S diagram characterizes an area of high plankton abundance. Thus, it appears that (a) the low plankton catches made close to the coast are the result of the intrusion of Intermediate water, and (b)

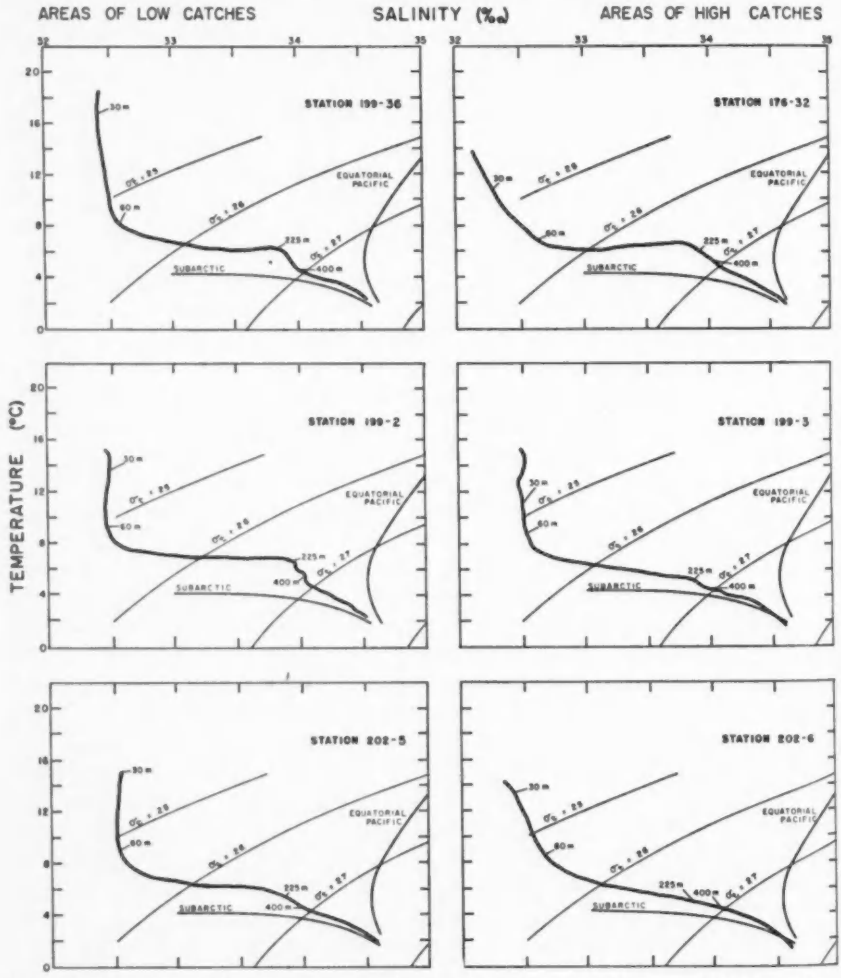

FIG. 10. Comparison of temperature-salinity diagrams from oceanic areas of high and low plankton catches.

the plankton catches increase accordingly in those northern areas which are less influenced by this intrusion.

Between Stations 9 and 11 of Cruise 199 there was a sharp drop in the abundance of plankton, a decrease related to changes in the physical and chemical conditions. Figure 11 shows T-S diagrams obtained at Stations 9, 10, 10A, and 11. The progressive importance of the Intermediate water is apparent and it parallels the 10-fold decrease in the plankton catches. Coincident with the occurrence of Intermediate water was the appearance of a temperature inversion at depths between 100 and 200 m. As noted previously, the plankton was

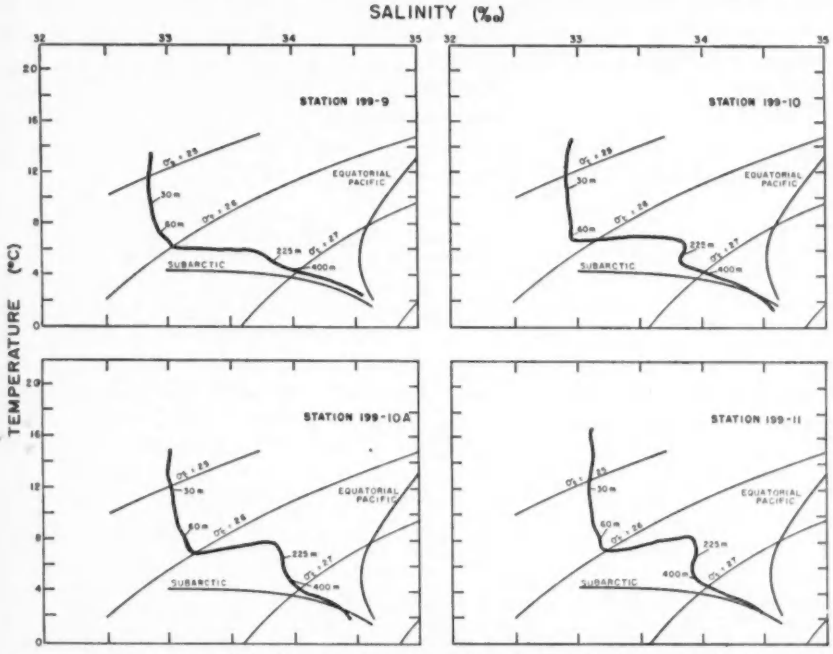

FIG. 11. Temperature-salinity diagrams from *Brown Bear* Cruise 199, Stations 9, 10, 10A and 11.

concentrated within the inversion. This fact results in a distortion of the standing crop estimate for the area as the highest catches of plankton occurred at depths not used in the estimate. For example, using only catches made at standard depths (30, 60, and 225 m) between Stations 11 and 12, the average catch was 3.1 ml/min of trawling. When the catches made in hauls taken within the inversion at depths of 120 and 160 m were included in the estimate the average catch increased to 9.4 ml/min. Further to the south the inversion became less prominent and the plankton were less concentrated within the inversion. Between Stations 12 and 13, the estimate based upon the catches made at standard depths was 2.8 ml/min; by including the catches made within the inversion the average catch was increased to 5.9 ml/min. Between Stations 13 and 14 the

inversion still occurred, but the water within the inversion was only about 0.1°C warmer than the overlying water. Here the average catch made in the standard hauls was 2.2 ml/min as opposed to a catch of 3.2 ml/min when the inversion catches were included in the average. The inversion disappeared between Stations 14 and 15 and inclusion of catches made at the same depths where the inversion was present at previous stations only reduced the standing crop estimate. The average catch made in the standard hauls was 4.3 ml/min, but it was only 3.9 ml/min if catches made at 120 and 160 m were included in the estimate.

Hauls made in the southernmost portion of the area sampled resulted in very low catches. Standing crop estimates for the waters off Southern California are only one-hundredth of those made at comparable longitudes off the Washington Coast. T-S diagrams from Stations 22, 23, and 24 (Fig. 12) shows the dominance of Equatorial water in this area and the much reduced significance of Subarctic water. The night catches in the southern waters were greatest in hauls made deeper than 60 m, usually at 120 to 400 m.

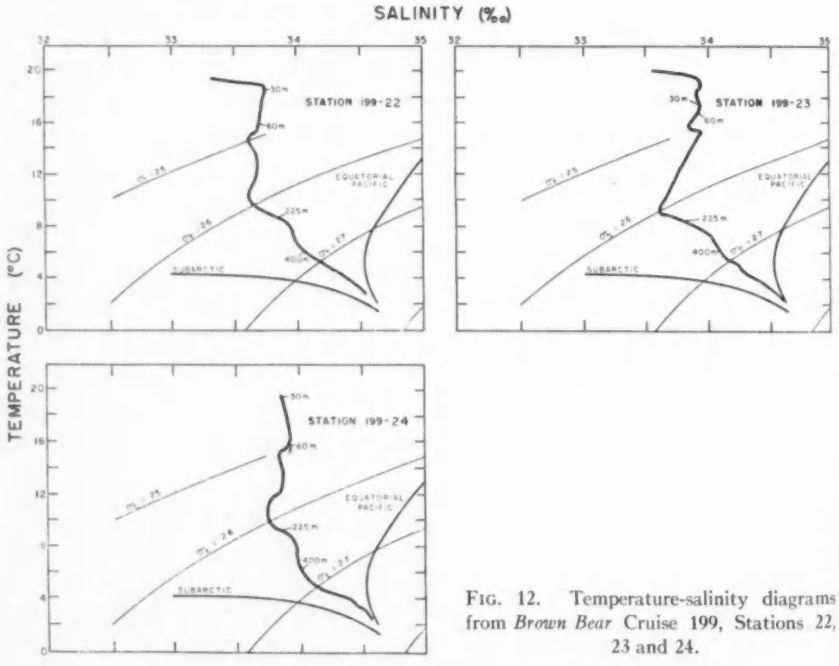

FIG. 12. Temperature-salinity diagrams from *Brown Bear* Cruise 199, Stations 22, 23 and 24.

Table VIII summarizes the depth distribution of the plankton catches according to area. This table is based on the accumulated oceanographic information obtained during the cruises; except for Area I it includes only the data obtained by using the 6-foot trawl.

TABLE VIII. Depth distribution of plankton catches according to area. (See below for description of areas. Haul 292 of Cruise 199 and Hauls 20 and 43 of Cruise 202 were not used in compiling this table because of plankton patchiness.)

Cruise No.	Area	Average volume of catch (*ml/min*)				
		20–30	31–60	61–120	121–250	251–400
176	A	43.7	12.7	4.3	5.8	No hauls
	B	12.9	28.2	17.8	10.8	No hauls
	C	18.3	7.7	No hauls	6.1	No hauls
199	D	0.6	6.1	No hauls	3.2	No hauls
	E	28.6	22.1	No hauls	7.8	No hauls
	F	1.8	3.4	6.2	5.1	No hauls
	G	0.9	1.0	4.0	1.7	1.2
	H	8.6	9.5	6.8	4.4	3.4
	I[a]	22.1	33.5	10.1	4.7	1.4
202	J	3.2	13.6	5.3	9.5	4.6
	K	8.7	9.5	14.2	9.7	8.4
		(2.2)[b]	(3.5)	(10.5)		(7.3)

[a]Average volumes are 3 times average volumes caught by 3-foot net.
[b]Numbers in parentheses are volumes excluding catches made in Hauls 73–79.

Cruise 176 is divided into three areas:

Area A — Offshore region, not influenced by Subarctic Current, between Stations 32 and 37, and between Station 29 and north of 49°N (Hauls 4–37 and 89–123). Hauls 91–99 were not considered because they were taken in Shelikof Strait.

Area B — Offshore region where Subarctic Current was apparent, those hauls south of 49°N (Hauls 124–148).

Area C — The Aleutian Island area (Hauls 38–86).

No significant penetration of Intermediate water was noted on Cruise 176.

Cruise 199 is divided into six areas:

Area D — Area just off the Washington Coast between Stations 1 and 3 where Intermediate water was present and the halocline temperatures were mostly above 6.0°C (Hauls 9–33).

Area E — Offshore region between Stations 3 and 10 of mostly Subarctic water with halocline temperatures mostly below 6.0°C (Hauls 34–95).

Area F — Offshore region between Stations 10 and 19 strongly influenced by presence of Intermediate water and some Central and Equatorial water with halocline temperatures above 7.0°C and as high as 10.0°C (Hauls 96–176).

Area G — Offshore southern region between Stations 21 and 30, similar in most respects to the previous region, but with greater quantities of Equatorial water, halocline temperatures, where the halocline was present, exceeding 8.0°C (Hauls 232–284).

Area H — Offshore region, between Stations 30 and 33, oceanographically intermediate between areas described in E and F, Intermediate water was present, the halocline temperatures were all below 8.0°C (Hauls 285–300).

Area I — Offshore region, between Stations 33 and 38, mostly Subarctic waters, but Intermediate water was present along the cruise track, halocline temperatures varied, but were all below 8.0°C and sometimes were less than 6.0°C. In this area, because of the failure of the main winch, only hauls with the 3-foot net were available for study (Hauls 301–328).

Cruise 202 is divided into two areas:

Area J — Offshore region between 49°N, 135°W and Station 7 of Subarctic water, with halocline temperatures mostly below 6.0°C (Hauls 16–27).

Area K — Offshore region between Station 4 and 49°N, 135°W and between Stations 7 and 14 influenced by presence of Intermediate water having halocline temperatures above 6.0°C (Hauls 6–15 and 33–79).

On Cruise 176 and in Areas D, E, and F, the deepest haul made routinely was at 225 m. In all other areas, new cable permitted routine sampling at depths to 400 m. Table VIII shows that the major changes in plankton abundance occurred in the shallow hauls; catches made in the deeper hauls were relatively constant. This, of course, closely parallels the physical and chemical environment which horizontally varies less at depth than in the surface waters. Even at the depths being considered, however, definite latitudinal variation is apparent. The smallest catches made in the 400-meter hauls were found furthest to the south in waters that had the lowest percentage of Subarctic water. These catches were only one-third to one-seventh the volume of catches made at the same depths in more northern waters. The low average catch of 1.4 ml/min made in the 400-meter hauls with the 3-foot net probably is the result of insufficient sampling and of escapement, for the plankton caught in deeper hauls are larger and probably faster-swimming than those taken in shallower depths.

The data from Cruise 202 obtained in the area influenced by Intermediate water are somewhat distorted by the inclusion of hauls made close to shore in the region where cool water pushes towards the surface (Fig. 5). The numbers shown in parentheses in Table VIII for this area are the average volumes of all hauls, not including those made close to shore. Removal of these hauls from consideration further emphasizes the fact of the concentration of plankton at depth and their absence in shallower water.

The preceding data show sharp and extensive quantitative variations which clearly relate to equivalent changes in the physical and chemical environment of the area under study. It can be shown that these variations occur also in species distribution. Table IX shows depth and area distribution for catches of the 7 commonest fish (all Myctophidae), the 3 commonest pteropods, and the commonest heteropod; except for Area I, these data were obtained with the 6-foot net. The distributions of 4 of the myctophids, the 3 pteropods and the heteropod are illustrated in Fig. 13.

Lampanyctus leucopsarus, the most abundant and most frequently caught fish on the surveys, was taken in almost every offshore haul north of 45°N except in those made in the upper 30 m in that area of Cruise 202 influenced by the extensive intrusion of Intermediate water. South of 45°N the species occurred in only 15 of 89 hauls. Only 3 of these occurrences were in hauls made in the upper 60 m, and these 3 records were all north of Station 11 (Cruise 199); south of Station 13 there were no catches at any depth, except in 3 hauls just west of Station 18. That the species is first eliminated in the shallow hauls is consistent with the physical and chemical data, for latitudinal gradients diminish with an increase in depth.

TABLE IX. Distribution of important animals by Area and depth. The "F" columns show the number of hauls containing the animal, and the total hauls made. The "N" columns show the average number of specimens taken in all hauls. The "Areas" indicated in the left-hand column are as follows:

Area	Cruise No.	Haul Nos.	Description
A	176	4–37 89–123	Offshore area not influenced by Subarctic Current between Stations 32 and 37 and between Station 29 and 49°N latitude.
B	176	124–148	Offshore area where Subarctic Current is apparent south of 49°N latitude.
C	176	38–86	The Aleutian Island Area.
D	199	9–33	Area just off the Washington Coast between Stations 1 and 3 with considerable Intermediate water present.
E	199	34–95	Offshore region between Stations 3 and 10, composed mostly of Subarctic water.
F	199	96–176	Offshore region between Stations 10 and 19, strongly influenced by the presence of Intermediate water and some Central and Equatorial water.
G	199	232–284	Offshore region between Stations 21 and 30, similar in most respects to the previous region, but with greater quantities of Equatorial water.
H	199	285–300	Offshore region, oceanographically intermediate between Areas E and F.
I	199	301–328	Offshore region, mostly Subarctic water, but Intermediate water is present along the cruise track.
J	202	16–27	Offshore region between 49°N, 135°W and Station 7 of Subarctic water.
K	202	6–15 33–79	Offshore region between Station 4 and 49°N, 135°W and between Stations 7 and 14 with considerable Intermediate water present.

Distribution of *Lampanyctus leucopsarus*

Area	20–30 *m*		31–60 *m*		61–120 *m*		121–250 *m*		251–400 *m*	
	F	N	F	N	F	N	F	N	F	N
A	9/10	55.7	10/10	17.9	3/3	4.3	12/12	6.3	No hauls	
B	6/6	20.0	5/5	43.6	3/3	10.6	9/9	8.6	No hauls	
C	4/9	88.5	8/9	18.5	No hauls		9/10	13.8	No hauls	
D	1/1	6.0	1/1	10.0	No hauls		1/1	3.0	No hauls	
E	8/8	93.5	11/11	26.3	No hauls		11/11	12.5	No hauls	
F	2/9	1.4	1/7	0.1	3/7	0.9	8/23	0.7	No hauls	
G	0/11	0.0	0/9	0.0	1/5	0.2	0/10	0.0	0/8	0.0
H	5/6	14.0	3/3	10.3	2/2	1.0	2/3	4.0	1/2	1.5
I	4/7	39.5	5/6	2.0	2/2	1.5	3/4	2.3	0/2	0.0
J	2/2	3.0	3/3	20.0	2/2	3.0	1/2	0.5	2/2	21.0
K	3/16	3.8	8/9	6.7	7/7	7.3	6/7	2.7	8/9	19.4

Distribution of *Diaphus theta*

A	6/10	13.6	4/10	1.7	3/3	1.0	7/12	1.1	No hauls	
B	5/6	3.7	5/5	4.0	2/3	2.0	6/9	1.4	No hauls	
C	2/9	0.6	2/9	0.8	No hauls		3/10	0.8	No hauls	
D	1/11	2.0	1/1	11.0	No hauls		1/1	7.0	No hauls	
E	8/8	19.4	10/11	5.1	No hauls		9/11	2.5	No hauls	
F	3/9	9.2	3/7	1.3	2/7	0.7	12/23	1.3	No hauls	
G	2/11	0.2	1/9	0.3	1/5	0.2	2/10	0.2	0/8	0.0
H	3/6	11.2	3/3	2.7	2/2	2.5	1/3	0.7	1/2	1.0
I	4/7	0.0	2/6	0.3	0/2	0.0	1/4	0.3	0/2	0.0
J	0/2	0.9	3/3	14.0	2/2	2.0	1/2	0.5	2/2	1.5
K	2/16	0.6	6/9	12.3	7/7	5.4	5/7	2.4	7/9	2.9

Distribution of *Tarletonbeania crenularis*

Area	20–30 m		31–60 m		61–120 m		121–250 m		251–400 m	
	F	N	F	N	F	N	F	N	F	N
A	2/10	1.4	1/10	0.1	0/3	0.0	3/12	0.3	No hauls	
B	3/6	0.5	4/5	1.8	2/3	1.3	7/9	0.9	No hauls	
C	1/9	0.1	1/9	0.1	No hauls		1/10	0.1	No hauls	
D	1/1	26.0	1/1	26.0	No hauls		1/2	13.5	No hauls	
E	7/8	8.1	11/11	3.5	No hauls		8/11	3.5	No hauls	
F	1/9	0.4	2/7	0.3	1/7	0.1	3/23	0.2	No hauls	
G	No captures in any hauls									
H	4/6	1.7	2/3	2.0	1/2	0.5	1/3	0.3	0/2	0.0
I	5/7	3.6	6/6	1.7	1/2	0.5	1/4	0.5	1/2	1.0
J	2/2	23.0	3/3	2.3	1/2	0.5	1/2	0.5	1/2	1.0
K	7/16	3.1	8/9	1.8	3/7	1.7	5/7	1.0	8/9	1.8

Distribution of *Electrona arctica*

A	3/10	0.3	2/10	0.8	0/3	0.0	10/12	5.1	No hauls	
B	0/6	0.0	0/5	0.0	0/3	0.0	3/9	1.9	No hauls	
C	1/9	0.1	2/9	0.2	No hauls		5/10	8.1	No hauls	
D	0/1	0.0	0/1	0.0	No hauls		0/1	0.0	No hauls	
E	0/8	0.0	0/11	0.0	No hauls		2/11	0.2	No hauls	
F	0/9	0.0	0/7	0.0	1/7	0.3	0/23	0.0	No hauls	
G	0/11	0.0	0/9	0.0	0/5	0.0	0/10	0.0	2/8	0.8
H	0/6	0.0	0/3	0.0	0/2	0.0	0/3	0.0	2/2	7.0
I	0/7	0.0	0/6	0.0	0/2	0.0	0/4	0.0	2/2	1.0
J	0/2	0.0	0/3	0.0	0/2	0.0	2/2	4.5	2/2	5.0
K	0/16	0.0	1/9	0.1	0/7	0.0	4/7	3.3	8/9	8.8

Distribution of *Electrona crockeri*

A	No occurrences in these areas									
B	No occurrences in these areas									
C	No occurrences in these areas									
D	0/1	0.0	0/1	0.0	No hauls		0/1	0.0	No hauls	
E	0/8	0.0	1/11	0.2	No hauls		1/11	0.1	No hauls	
F	2/9	0.2	4/7	2.6	1/7	0.1	18/23	3.7	No hauls	
G	0/11	0.0	3/9	0.6	1/5	0.4	5/10	5.4	6/8	2.0
H	0/6	0.0	0/3	0.0	1/2	1.0	2/3	1.3	2/2	1.0
I	0/7	0.0	0/6	0.0	0/2	0.0	1/4	0.3	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	0/2	0.0	0/2	0.0
K	1/16	0.1	0/9	0.0	0/7	0.0	2/7	0.3	0/9	0.0

Distribution of *Ceratoscopelus townsendi*

A	No occurrences in these areas									
B	3/6	1.3	2/5	0.4	No hauls		0/9	0.0	No hauls	
C	No occurrences in these areas									
D	No occurrences in these areas									
E	No occurrences in these areas									
F	7/9	19.1	6/7	3.4	3/7	2.0	11/23	0.8	No hauls	
G	9/11	4.9	8/9	5.9	5/5	4.8	6/10	1.1	4/8	0.6
H	5/6	1.8	0/3	0.0	1/2	1.0	0/3	0.0	1/2	1.0
I	1/7	0.1	1/6	0.2	0/2	0.0	0/4	0.0	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	0/2	0.0	0/2	0.0
K	1/15	0.1	1/9	0.1	1/7	0.1	1/7	0.1	0/9	0.0

Distribution of *Lampanyctus ritteri*

Area	20–30 m		31–60 m		61–120 m		121–250 m		251–400 m	
	F	N	F	N	F	N	F	N	F	N
A	No occurrences in the area in 35 hauls									
B	0/6	0.0	1/5	0.4	2/3	2.0	5/9	0.9	No hauls	
C	0/9	0.0	0/9	0.0	No hauls		1/10	0.2	No hauls	
D	0/1	0.0	0/1	0.0	No hauls		0/1	0.0	No hauls	
E	0/8	0.0	3/11	0.8	No hauls		7/11	1.5	No hauls	
F	6/9	1.9	7/7	13.4	6/7	7.1	22/23	5.3	No hauls	
G	3/11	2.1	6/9	9.0	4/5	9.2	9/10	3.8	7/8	5.4
H	1/6	0.2	3/3	2.0	1/2	1.0	1/3	1.0	2/2	1.0
I	0/7	0.0	0/6	0.0	1/2	0.5	1/4	0.3	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	1/2	1.0	0/2	0.0
K	0/16	0.0	0/9	0.0	1/7	0.1	4/7	1.0	3/9	0.7

Distribution of *Limacina helicina*

A	5/10	2.2	4/10	1.1	1/3	0.3	5/12	1.0	No hauls	
B	0/6	0.0	1/5	0.8	0/3	0.0	1/9	0.3	No hauls	
C	5/9	4.3	4/9	9.3	No hauls		7/10	3.8	No hauls	
D	1/1	7.0	1/1	47.0	No hauls		1/1	28.0	No hauls	
E	3/8	0.6	7/11	4.9	No hauls		6/11	2.3	No hauls	
F	0/9	0.0	1/7	0.8	2/7	0.5	5/23	1.3	No hauls	
G	0/11	0.0	0/9	0.0	0/5	0.0	0/10	0.0	0/8	0.0
H	0/6	0.0	2/3	1.3	1/2	0.5	0/3	0.0	1/2	0.5
I	2/7	9.1	3/6	3.6	1/2	0.5	0/4	0.0	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	1/2	0.5	0/2	0.0
K	9/16	2.9	5/9	9.3	4/7	1.7	3/7	1.0	4/9	1.0

Distribution of *Cavolinia globulosa*

A	0/10	0.0	0/10	0.0	0/3	0.0	0/12	0.0	No hauls	
B	0/6	0.0	0/5	0.0	0/3	0.0	0/9	0.0	No hauls	
C	0/9	0.0	0/9	0.0	No hauls		0/10	0.0	No hauls	
D	0/1	0.0	0/1	0.0	No hauls		0/1	0.0	No hauls	
E	0/8	0.0	0/11	0.0	No hauls		0/11	0.0	No hauls	
F	0/9	0.0	0/7	0.0	3/7	3.0	8/23	9.9	No hauls	
G	0/11	0.0	3/9	0.3	4/5	10.4	3/10	2.3	4/8	12.5
H	0/6	0.0	0/3	0.0	0/2	0.0	0/3	0.0	0/2	0.0
I	0/7	0.0	0/6	0.0	0/2	0.0	0/4	0.0	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	0/2	0.0	0/2	0.0
K	0/16	0.0	0/9	0.0	0/7	0.0	0/7	0.0	0/9	0.0

Distribution of *Euclio pyramidata*

A	0/10	0.0	1/10	0.1	0/3	0.0	0/12	0.0	No hauls	
B	0/6	0.0	0/5	0.0	0/3	0.0	0/9	0.0	No hauls	
C	0/9	0.0	0/9	0.0	No hauls		0/10	0.0	No hauls	
D	1/1	3.0	1/1	3.0	No hauls		1/1	10.0	No hauls	
E	2/8	0.3	5/11	1.4	No hauls		1/11	0.1	No hauls	
F	2/9	1.1	6/7	2.7	5/7	22.4	14/23	3.0	No hauls	
G	7/11	5.3	6/9	3.6	5/5	6.4	8/10	3.3	5/8	3.0
H	2/6	1.3	1/3	0.6	0/2	0.0	1/3	1.0	0/2	0.0
I	2/7	2.5	2/6	0.6	0/2	0.0	0/4	0.0	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	0/2	0.0	0/2	0.0
K	6/16	1.5	4/9	1.3	3/7	0.5	2/7	0.2	2/9	0.6

Distribution of *Atlanta sp.*

Area	20–30 m		31–60 m		61–120 m		121–250 m		251–400 m	
	F	N	F	N	F	N	F	N	F	N
A	0/10	0.0	0/10	0.0	0/3	0.0	0/12	0.0	No hauls	
B	0/6	0.0	0/5	0.0	0/3	0.0	0/9	0.0	No hauls	
C	0/9	0.0	0/9	0.0	No hauls		0/10	0.0	No hauls	
D	0/1	0.0	0/1	0.0	No hauls		0/1	0.0	No hauls	
E	0/8	0.0	1/11	0.1	No hauls		1/11	0.1	No hauls	
F	7/9	14.3	6/7	8.0	6/7	6.1	20/23	7.7	No hauls	
G	11/11	34.0	9/9	9.2	4/5	17.2	9/10	10.3	8/8	8.8
H	2/6	6.0	1/3	1.0	1/2	1.5	0/3	0.0	0/2	0.0
I	0/7	0.0	0/6	0.0	0/2	0.0	0/4	0.0	0/2	0.0
J	0/2	0.0	0/3	0.0	0/2	0.0	0/2	0.0	0/2	0.0
K	0/16	0.0	0/9	0.0	0/7	0.0	0/7	0.0	0/9	0.0

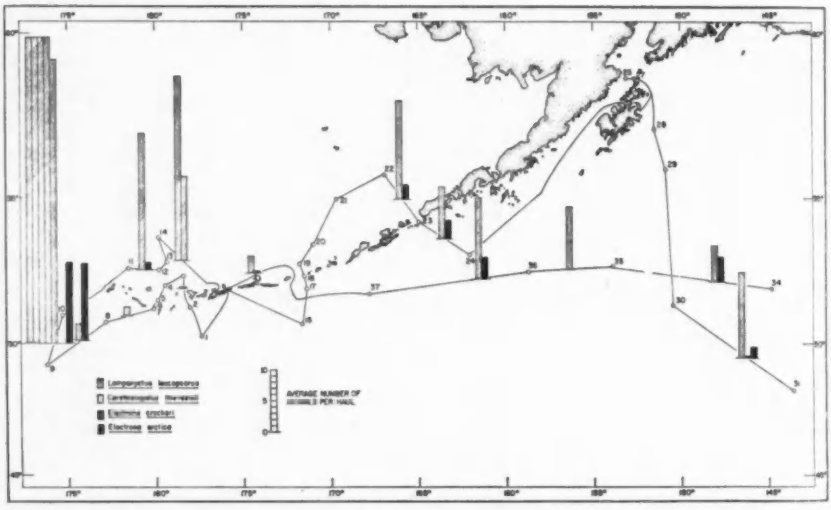

FIG. 13a. Cruise tracks showing position of hydrographic stations and the average catch of several common fishes taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 176.

North of 45°N, it is the vertical distribution of the species that reflects physical and chemical conditions; generally the abundance of the species was greatest in the upper 30 m and decreased with depth. As mentioned in the section on vertical migration, the Subarctic Current appears to suppress the migration of the species. During the last part of Cruise 176 (Hauls 124–148) the peak abundance of the species occurred at about 60 rather than at 30 m. The actual abundance of the species per unit area did not change; the sum of the average catches per haul at all depths was 84.2 for the offshore portion of the cruise not influenced by the Subarctic Current, and 82.8 for the area influenced by the Subarctic Current.

During Cruise 202 a combination of the influence of Intermediate water and the Subarctic Current appeared to interact. During both legs of this cruise low catches were made in the upper 30 m. In that portion influenced by the Intermediate water, peak catches occurred within the halocline; on the other leg the peak catch occurred above the halocline. The average catch at all depths, excluding the 400-meter hauls, was 20.5 for the area with Intermediate water and 26.5 for the more typically Subarctic water. The high averages

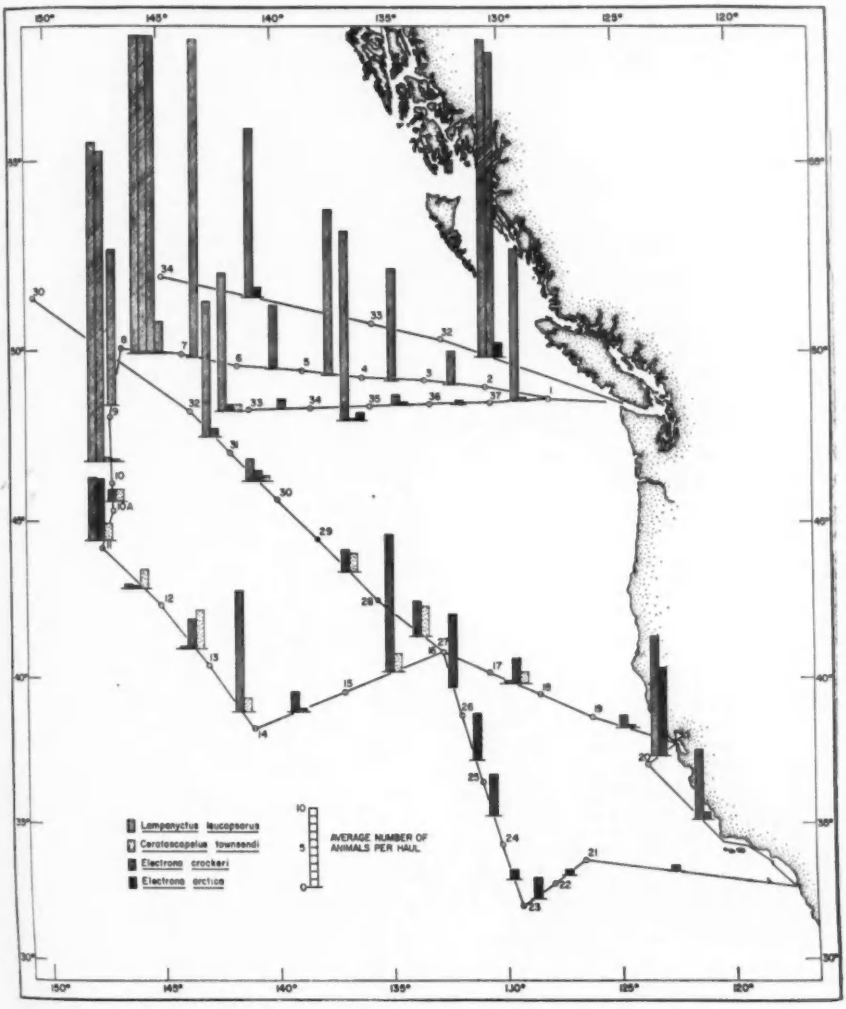

FIG. 13b. Cruise tracks showing position of hydrographic stations and the average catch of several common fishes taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 199.

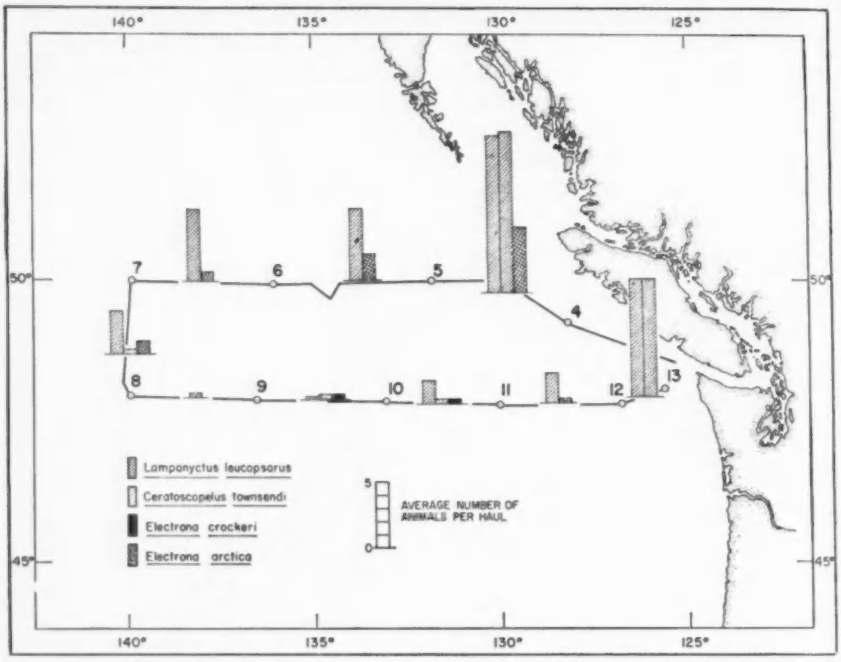

FIG. 13c. Cruise tracks showing position of hydrographic stations and the average catch of several common fishes taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 202.

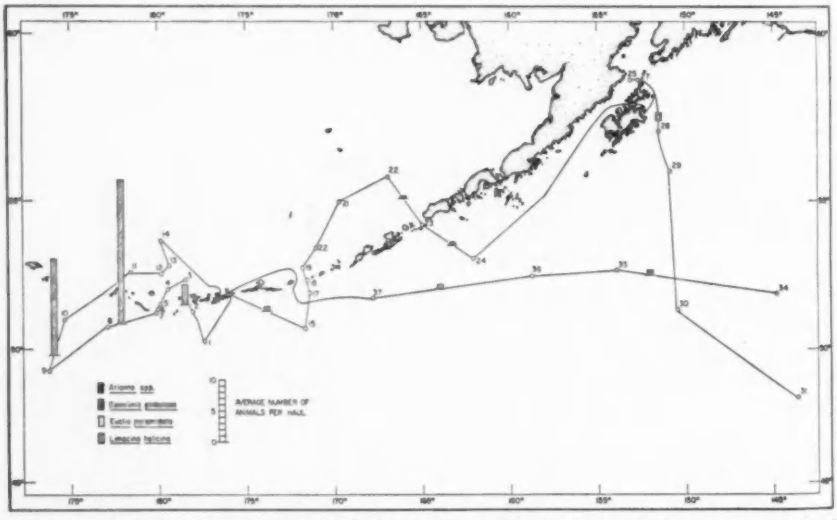

FIG. 13d. Cruise tracks showing position of hydrographic stations and the average catch of a heteropod and 3 pteropods taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 176.

obtained for the 400-meter hauls were probably sampling artifacts because these hauls were made at a time when the animals had begun their downward migration. These data are further distorted by the catch of 82 fish in a single haul (Haul 73) close to shore in an area where cold water pushes towards the surface.

The distribution of *Diaphus theta* (Table IX) was much like the distribution of *L. leucopsarus*, except for *D. theta*'s infrequent occurrence in the Aleutian Island region and its wider southern range. South of 45°N the species occurred

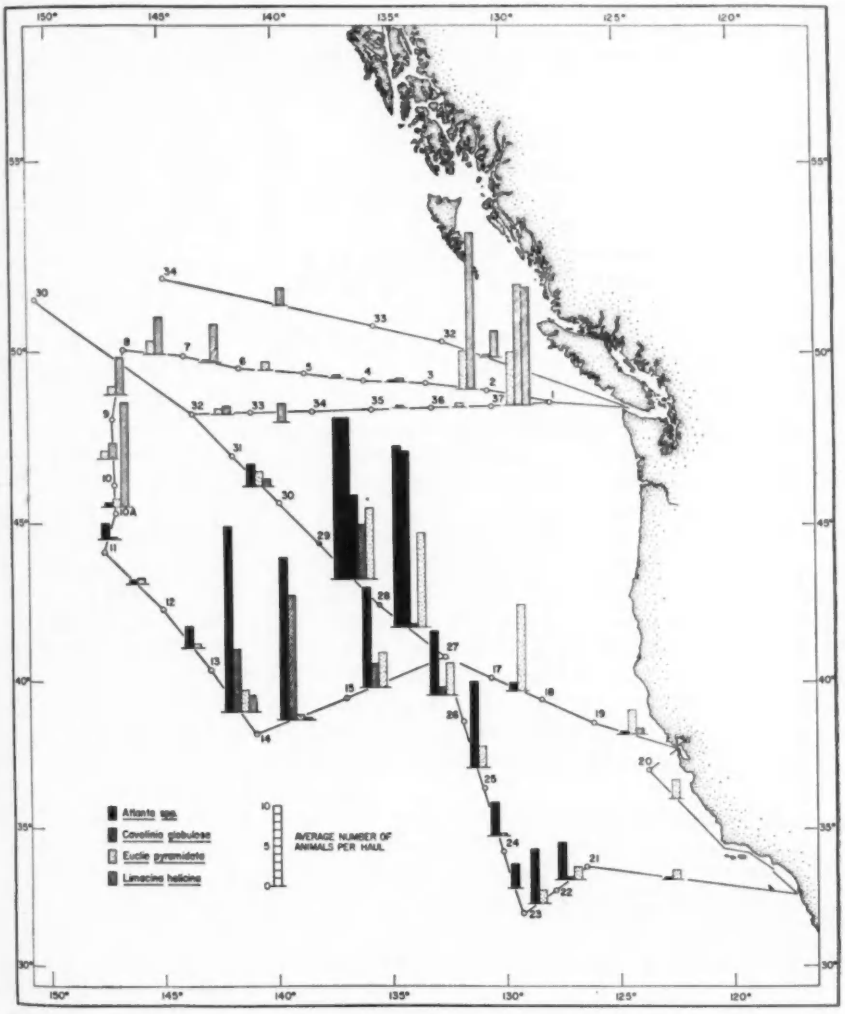

FIG. 13e. Cruise tracks showing position of hydrographic stations and the average catch of a heteropod and 3 pteropods taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 199.

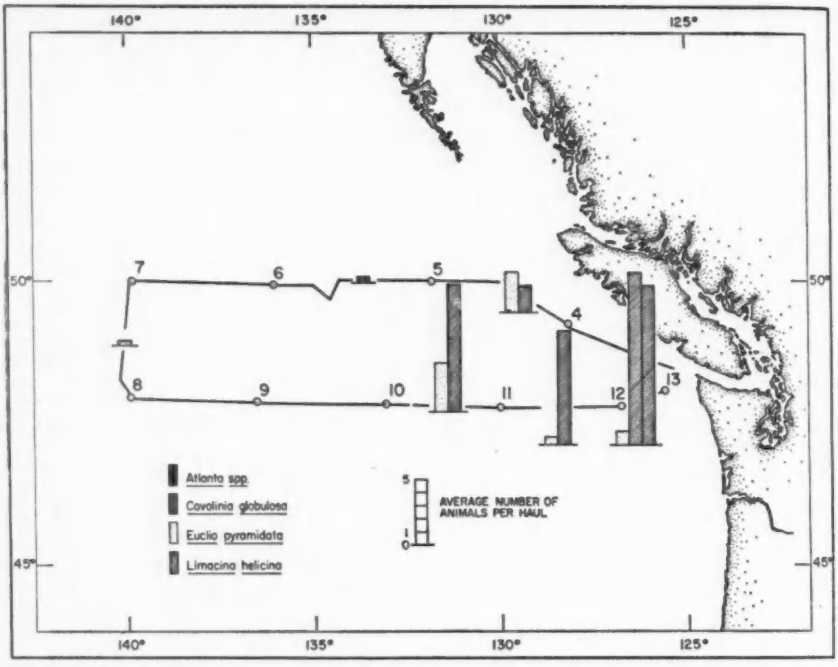

FIG. 13f. Cruise tracks showing position of hydrographic stations and the average catch of a heteropod and 3 pteropods taken at depths of 30, 60 and 225 meters. *Brown Bear* Cruise 202.

in only 26 of 89 hauls, 9 of these being in the upper 60 m. *D. theta* did not occur in hauls in the upper 60 m in offshore waters south of Station 13, although it appeared in the deeper hauls occasionally throughout the sampling area. In areas apparently influenced by the Subarctic Current, *D. theta*, like *L. leucopsarus*, was most abundant in hauls made deeper than 30 m, whereas it was abundant in the upper 30 m in those areas not influenced by the Subarctic Current. The influence of Intermediate water on the vertical distribution of *D. theta* is less pronounced than for *L. leucopsarus;* however, where Intermediate water occurred north of 45°N, relatively high catches of *D. theta* were made in and below the halocline.

Tarletonbeania crenularis occurred less frequently than either *D. theta* or *L. leucopsarus*. Its pattern of distribution (Table IX) closely resembles *D. theta*. The very low numbers of *T. crenularis* in the northernmost parts of the survey area is probably a function of inadequate sampling rather than its actual absence from the area. The species was extremely common throughout the area north of 45°N at all stations when night-light observations were possible. Mr R. LeBrasseur[7] reports this species to be the most common fish taken in hauls made with a midwater trawl towed at the surface in the Gulf of Alaska. The fact

[7]Personal communication; Fisheries Research Board of Canada, December 1959.

that no surface tows were attempted in the area during our surveys probably distorts our horizontal distribution data for the species.

All specimens of *Tarletonbeania* taken during the cruises have been identified as *T. crenularis*. Wisner (1959) places the northern boundary of *T. crenularis* at about 50°N, so it is possible that those *Tarletonbeania* taken to the north of this line are actually *T. taylori*. However no adult male fish were taken and the criteria are questionable for distinguishing immature or female *T. taylori* from *T. crenularis*.

Regardless of the specific identification, *Tarletonbeania* almost completely disappeared south of 45°N, occurring in only 7 out of 89 hauls. With the exception of 2 hauls close to Station 18 the genus was absent from the offshore area south of Station 11.

The two species of *Electrona*, *E. arctica* and *E. crockeri* (Table IX), are both primarily deep dwellers. They occurred only rarely in hauls made in the upper 120 m, but the genus is represented in most of the deep hauls. The distribution of the two species is complementary. North of 45°N, *E. arctica* occurred in 40 of the 74 hauls made at depths greater than 120 m. South of 45°N the species occurred in only 2 of 41 hauls, both in hauls made at 400 m. North of 45°N, *E. crockeri* occurred in only 8 of 74 hauls, but south of this latitude the species appeared in 29 of 41 hauls. During the surveys both species occurred in the same haul only 5 times and these were all in hauls made at a depth of 400 m.

Ceratoscopelus townsendi, a resident of the upper waters, and *Lampanyctus ritteri*, a species with a wide vertical range, have distributions which complement the distributions of *L. leucopsarus* and *D. theta* (Table IX): north of Station 10 they were found rarely, but south of that station they occurred in the majority of hauls. The capture of two specimens of *L. ritteri* near the tip of the Aleutian Islands (Haul 68, Cruise 176) seems anomalous until it is realized that this area is probably in the path of the Subarctic Current and that the only northern areas in which *L. ritteri* appeared with any degree of regularity were those sections influenced by the Subarctic Current. The wide vertical distribution of *L. ritteri* paralleled its relatively wide horizontal range, although its peak concentrations occurred towards the southern parts of the survey area. *C. townsendi*, with more restricted vertical distribution, is likewise limited horizontally. It occurred in 72 of the offshore hauls but in only 19 of these did it occur with *L. leucopsarus*, a species taken in 213 of the offshore hauls. All 19 occurrences are in waters of physical and chemical transition.

A number of other fish species, not listed in the table, had distributions limited to particular water masses. The lantern fishes *Diogenichthys atlanticus* and *Myctophum californiense* were primarily concentrated in waters influenced by the presence of Intermediate, Central and Equatorial water and were very rare in the Subarctic waters. Likewise concentrated in the south were other pelagic fishes such as *Idiacanthus antrostomus*, *Argyopelecus heathi*, *A. olfersi*, *Melamphaes lugubris*, *M. bispinosus*, *Rhectogramma sherbourni*, and *Bathylychnops exilis*. Only a few species, such as *Lestidium ringens* and *Chauliodus macouni*, seemed confined to the Subarctic water in the north. The distribution of *C.*

macouni was noted by Haffner (1952) to be limited to the Gulf of Alaska and the waters off the coast of California.

The distributional patterns shown by the fish are repeated by all of the few invertebrates which have been investigated. Table IX gives the distribution of the 3 most abundant pteropods (*Limacina helicina*, *Cavolinia globulosa* and *Euclio pyramidata*) and the most abundant heteropod genus (*Atlanta*).

Limacina helicina (Table IX) has a distribution like *L. leucopsarus* and the other Subarctic-dwelling pelagic fishes. It occurred in only 8 of the 89 offshore hauls taken south of 45°N, occurring only once in the upper 60 m. No captures of this species were made south of Station 15. Captures north of 45°N are recorded in 72 of 214 hauls, with the species occurring most frequently in those areas having the highest percentage of Subarctic water.

Cavolinia globulosa (Table IX) appeared only in hauls made south of Station 13 (Cruise 199), and its distribution definitely seems related to the distribution of Equatorial water. Tesch (1948) finds that this species, "... is practically confined to the tropical belt of the Indo-Pacific". A point of interest was the capture of 565 specimens in a 30-minute daytime haul (Haul 138) at a depth of 60 m, latitude 38°36′N. The largest catch of the species previously reported by Tesch (made with a 2-meter stramin net) was 313 specimens per hour of towing at 3°40′N.

Euclio pyramidata (Table IX) occurred in greatest numbers south of Station 10, where it was found in 58 of 89 hauls. Its northern range was primarily restricted to those areas influenced by Intermediate water; as the percentage of Subarctic water increased the catch of *E. pyramidata* decreased. No captures of this species were made in the Aleutian Islands region.

The identification of the species of the heteropods in the genus *Atlanta* is uncertain, probably at least two species being represented in our collection. Regardless of species identification, however, the genus (Table IX) was present in only 6 hauls made north of Station 10. It appeared in nearly all of the hauls south of Station 10 and increased in abundance with increased percentage of Central and Equatorial water.

Two species of *Gnathophausia*, a bathypelagic mysid, have a complementary distribution. *G. ingens* was recorded only in hauls taken south of 45°N, while *G. gigas* was limited to the deep hauls made to the north of this latitude.

Of special interest was the occurrence of a number of new species, as well as new records of species being taken far from their previously known geographic range. Captured during the surveys were: *Bathophilus flemingi*, a new species of stomiatoid, (Aron and McCrery, 1958); *Astronesthes nigroides*, another new stomiatoid, (Gibbs and Aron, 1960); a melamphid in the genus *Melamphaes*[8], and what appears to be a new chiasmodontid in the genus *Pseudoscopelus*. Also recorded were a number of myctophids which may represent new species in the genera *Lampadena*, *Diaphus*, *Electrona* and *Notoscopelus*. The *Electrona* fits

[8]Personal communication from Mr Alfred Ebeling, Scripps Institution of Oceanography, February 1959.

the extreme range of *E. rissoi* and has been tentatively identified as that species, but Dr Rolf Bolin expresses some doubts[9], believing that further study may reveal these fish as a new species.

Species whose captures during the surveys represent major range extensions included: the pelagic apogonid, *Rhectogramma sherborni*, previously recorded from the Atlantic Coast of Africa; *Photonectes margarita* and *Melanostomias biseriatus*, both stomiatoids and both previously recorded only from the western Atlantic; and *Opostomias mitsuii*, another stomiatoid, known from only 2 specimens taken near Japan.

It is of ecological significance that all of the major range extensions mentioned above, as well as the capture of the questionable *Electrona* (if it is *E. rissoi* it would become the only Pacific myctophid with a bipolar distribution) and a number of specimens of *Bathylychnops exilis* (known previously from a single specimen), were made in about the same area, at about 40°N latitude. In this area a band of Central water from the south interleaves between the deeper Intermediate water and the overlying halocline. The narrow depth range of this band may serve to confine species that usually occur at greater depth, thus making them susceptible to capture.

CONCLUSIONS

In spite of the limited data available, biological variations can be associated with variations in the physical and chemical characteristics of the area under consideration. The following general conclusions have been reached:

1. In areas of neutral stability or high turbulence the standing crop is low. This probably indicates a low rate of productivity, resulting from the increased time phytoplankton spend below the compensation depth in the turbulent areas.

2. The diurnal migrations of plankton and some fishes are affected by the physical and chemical environment. In the region of Subarctic water not influenced by the Subarctic Current the peak abundance of animals was found in the upper 30 m. Where the Subarctic water mass was overlayed by the waters of the Subarctic Current the diurnal migration of animals was suppressed, the peak abundance occurring at a depth of about 60 m. In both cases the peak abundance of animals occurred at about the same depth as the 50°F (10°C) isotherm. In areas where Intermediate water intruded into the Subarctic water mass the halocline served as a partial barrier to migration; peak abundances of animals were found below the top of the halocline. Temperature inversions also modify the diurnal migration patterns. In the region of an extensive inversion the plankton were concentrated within, but not above or below, the inversion. As the temperature gradient of the inversion diminished, the concentration of plankton within the inversion also diminished.

In all of the above examples the modifying influences are demonstrated by reference to temperature and salinity. These variables, however, are only

[9]Personal communication, Hopkins Marine Station, July 1959.

used for convenience. Variations in temperature and salinity distributions are indicative of other, and probably more biologically significant, physical and chemical changes. Diurnal migrants under usual conditions pass through much larger temperature and salinity changes during their vertical travels than are being considered in the examples. It is possible that the gradients involved are of prime importance, but inadequate understanding of the basic physiology of the planktonic animals makes further discussion of this point superfluous.

3. In 1957 the standing crop of plankton diminished with increasing distance from the Washington coast. The high standing-crop estimated for the area just south of the Alaska Peninsula occurs at the transition between the Alaska Coastal region and the Alaskan Gyral. The 1958 standing-crop estimates, made close to the Washington coast, were about 10 times less than estimates made for the same area in the previous year. The low standing-crop occurred where Intermediate water had intruded into the Subarctic water mass. As the influence of the Intermediate water diminished and the percentage of Subarctic water increased in the sampling region, the standing crop also increased.

4. In the open ocean the transition from Subarctic water to Intermediate water was marked by abrupt changes in both quantities and kinds of animals. The quantitative change was by a factor of 10 and the qualitative change was such, at least for the animals that have been identified to species, that there was very little species overlap between the two oceanographic regimes.

5. In the most southerly part of the survey area, a region characterized by considerable quantities of Central and Equatorial waters, the standing-crop estimates were 100-fold less than at similar longitudes off the Washington Coast.

6. Where a band of Central water interleaved between the deeper Intermediate water and the surficial halocline water, a number of new species occurred, together with significant range extensions of previously described species. The narrow depth-range of this band may have served to confine species that usually occur at greater depths, thus making them susceptible to capture.

Future studies might well be divided into two phases: (1) a more complete analysis of the data already obtained, and (2) continued exploration of the area for further study of existing conditions and a quantitative evaluation of the sampling equipment.

Under the first phase the more pressing problems include:

a. Identification of the invertebrates to species and a study of their distribution in relation to the physical and chemical environment. Of particular importance appear to be the euphausiids, amphipods, and pelagic shrimps. These three groups are all well represented in the collections and, from the quantitative point of view, are probably better sampled than the species used in this study. Particularly amenable to analysis are the euphausiids which, because of the studies by Boden *et al.* (1955), present the least taxonomic difficulties.

b. Identification of the fish larvae to species with a study of their distribution in relation to the physical and chemical oceanography of the area.

c. Identification of the remaining unidentified adult fish, including an analysis of the specimens of *Tarletonbeania* to better elucidate the problem posed by Wisner (1959).

Under the second phase the following problems should be considered:

a. A critical examination of the biological, physical, and chemical changes in the transition regions. These studies could be simplified by the abrupt changes in the biology which are easily and quickly detected in the field.

b. A study of the seasonal and year-to-year changes in a plankton population. This is an especially difficult problem because of the unpredictable meanderings of currents and water masses. To obtain an estimate of the population parameters of a plankton community in the open ocean, preliminary work should be done in a smaller, more easily sampled area (such as a portion of Puget Sound).

c. A study of the fishing power of the trawls. This would allow the trawl catches to be placed on an absolute rather than a relative basis, thus permitting comparisons between the trawl and other standard plankton-sampling devices.

d. Detailed studies of diurnal migration. Rates of migration and the depth of peak abundance during the daylight hours should be determined.

The modified Isaacs-Kidd midwater trawl stands as one of our best tools in the investigation of the macroplankton and the small nekton. The close relationship between the physical and chemical observations and the biological data obtained through the use of the trawl is a strong point in favor of the continued use of the gear in future studies of oceanic ecology.

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Many people generously contributed their time and knowledge in the identification of the animals in the collection upon which this report is based. The lists of specialists and the groups in which they proved most helpful is given below as only a partial expression of the author's gratitude. In some cases all of the specimens of the group in our collection were examined by the specialist; in other cases, however, only a portion of the material was forwarded for study. Any errors of identification are, of course, the author's responsibility.

Elbert Ahlstrom	Bureau of Commercial Fisheries	Larval fishes
Rolf Bolin	Stanford University	Myctophids
William Clarke	Scripps Institution of Oceanography	Mysids
Daniel Cohen	Bureau of Commercial Fisheries	Argentinoids
Alfred Ebeling	Scripps Institution of Oceanography	Melamphaids and bathypelagics in general
Robert Gibbs	Boston University	Stomiatoids
Marion Grey	Chicago Natural History Museum	Gonostomids
Ernest Lachner	United States National Museum	Apogonids
N. B. Marshall	British Museum	Scopelarchids
John McGowan	Scripps Institution of Oceanography	Pteropods and Heteropods
Giles Mead	Harvard University	Scopelarchids
James Morrow	Yale University	Stomiatoids
Arthur Welander	University of Washington	Bathypelagics in general
Robert Wisner	Scripps Institution of Oceanography	Myctophids

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Tag Failure Associated with a Net Fishery as a Source of Experimental Error[1, 2]

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ABSTRACT

Tags may be forcibly separated from the fish by the action of the gear with which it is recaptured. This problem was evaluated by both tagging and removing the adipose fin on maturing chinook salmon (*Oncorhynchus tshawytscha*) and sampling in the gill net catches. In this study, a maximum estimate of error necessitating a correction coefficient of 1.196 is indicated. Error of this magnitude is of serious consequence to estimates of vital statistics of populations subject to high rates of exploitation.

INTRODUCTION

The use of tagged members of a fish population is considered to be a valuable approach for estimating various facets of the fishes biology, and population dynamics, yet the method has certain limitations, one of which is that the tag must remain intact. Failure of the tag to remain with the fish may result from structural failure of the materials used, a subject which has received some recent attention (Calhoun *et al.*, 1951; Forrester and Ketchen, 1955; Jensen, 1958). The tag may also be forcibly separated from the fish by the action of the gear with which it is recaptured (i.e., gill nets or seines) and in the writer's experience it is not unusual to receive a tag from a fisherman with the report that it was found tangled in the net, in the bottom of the net-hold, etc., with no knowledge of the fish to which it was formerly affixed. This type of failure leads to alternative possibilities. (1) The tagged fish may be recapture but remain undetected. (2) The tag may be recovered but the fish escape. These two possibilities affect conclusions about recapture in opposing directions. (3) Both the tag and the fish may be recovered even though separated by the recapture process. This latter possibility would introduce no serious error in deductions based on release-recovery data.

In 1952 an unusual opportunity to assess this type of error became available with a tagging experiment conducted in conjunction with a chinook salmon (*Oncorhynchus tshawytscha*) gill net fishery in the estuary of the Taku River, Alaska. For this particular year the entire chinook catch was handled by a single buying vessel, making it possible for an observer to examine the entire

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catch. Being stationed aboard the buyer the observer was also able to personally contact each fisherman as the catch was sold.

While the programme was not primarily designed toward this objective, and some of the features (viz., tag used, species of fish, etc.) cannot be directly extrapolated to other tagging experiments, this study can serve as an example of the possible effect of this type of error on an experiment using the technique of tagging.

MATERIALS AND METHODS

Three commercial trollers were chartered for the period May 10–25, 1952, to obtain chinook salmon prior to their entrance into the gill net area. A total of 555 fish suitable for tagging was obtained. To these, Petersen disc tags were affixed to the upper jaw. An inner plastic baffle, $\frac{3}{8}$-inch diameter (9.5 mm) was placed next to the head of a pure nickel pin. The pin was then inserted upward through the snout so that the baffle lay just posterior to the oral flap. The pin was directed at an anterior-dorsal angle. A $\frac{5}{8}$-inch diameter (15.9 mm) white baffle bearing identification and the serial number was then threaded over the pin and the pin cut and bent into a knot. The tag was put on rather tightly as no muscular tissue was enclosed. In addition the fish was marked by amputation of the adipose fin. A small patch of scales was removed from the region immediately above the lateral line and diagonally ventro-posteriorly from the insertion of the dorsal fin. Fork length was recorded to the nearest $\frac{1}{2}$ inch. (12.7 mm). The fish was then released. The tagging operation was accomplished with the fish immersed in sea water.

As previously stated, an observer was stationed aboard the buying vessel which serviced the gill net fleet during the fishing season, May 1–30. As catches were landed, fish showing a missing adipose fin were set aside for examination for evidence of having been previously tagged. Each fisherman was routinely asked about tagged fish being caught and tags reported. No difficulty was experienced in determining the former presence of a tag on fish with a missing adipose.

Scales were mounted dry between 2 × 2 inch glass slides and the edges bound with cellulose tape. These mounts were then placed in a photographic enlarger and negative prints made by direct projection onto glossy print photographic paper; thus enlarged images, approximately 3 × 4 inches, were obtained for further study. In addition, plastic impressions of the scale surface were made for projecting images of 100 diameters for the purpose of circuli counts and other detailed studies.

Tagged fish were recovered from other areas as will be noted. The migrating population was sampled by set net and fish wheel 17 miles above the mouth of the Taku River. Spawned out chinook carcasses were examined on one tributary of the system, the Nakina River in northern British Columbia. Recoveries from areas other than Taku were received from fishermen and fisheries agencies in southeastern Alaska and British Columbia. No observations of tag loss were made in these latter areas.

RESULTS

A summary listing of recoveries and observations is presented in Table I. It is apparent that many cases existed where the fish and tag were separated when entangled in the gill nets. In the upriver sampling, 17 fish were caught and landed with a set net with the tag intact; however, in 4 cases the fish escaped, leaving behind the tag. No fish were taken with a missing adipose, but which had previously lost their tag. On the spawning grounds, 8 fish were recovered with tags intact. No fish were observed without tags but with a missing adipose fin. The fish with intact tags were landed in mid-June by the Taku gill net fleet. These are included with other areas as no observations were made for missing tags at that time. Of 16 fish recovered by the gill net fishery with missing tags, 2 had incomplete tags, i.e., the wire and inner baffle were present but the identifying baffle was missing. Of the 10 tags recovered unattached to fish, 1 was reported as recovered from the bilge, 9 were found entangled in the nets.

TABLE I. Recoveries of marked and tagged chinook salmon.

Recovery area	Tag affixed to fish		Previously tagged	Tag only
	Complete	Incomplete		
Taku River				
Gill net fishery	34	2	14	10
Upriver sampling	17	0	0	4
Spawning ground	8	0	0	
Other areas	25	0	0	0

A question is posed concerning the 10 unattached tags and 14 fish which lost their tags. Were the 10 unattached tags from th 14 tagless but troll-marked fish in the catch, or were they from fish which lost ther tags in a contact with the nets but subsequently escaped and did not enter the catch? To answer this question it was attempted to deduce the original tag number of the 14 fish which had lost their tags by using length and scale data. Firstly, troll tagging and sampling in the gill net fishery ran concurrently, thus only fish tagged on or prior to the day of recapture need to be considered. Further reduction of possibilities can be made from considerations of the length of the fish concerned.

When tagged, each fish was measured by holding it up to a rule affixed at the water line of the tagging box. Since these were live fish, one might expect a minimum length due to muscle tonus and the possibility that the fish was not held perfectly straight. Measurements of fish landed by the gillnetters were made by laying the fish on a measuring cradle. While considerably more accurately is to be expected with this latter group, the fish themselves were in various stages of rigor mortis and relaxation. A comparison of original and second measurements of the 34 fish recovered with intact tags is presented in Table II. There is a tendency for fish to measure longer when dead than when supported alive in water, however, the differences are generally small being (with one exception) no greater than ½-inch. A fish which measured 1.5 inches

(38 mm) longer at the second station is considered to be an error in recording. Thus the possible list of fish tagged can be restricted by the landing length ± ½ inch. Within the remaining possibilities, certain fish were eliminated by their age as deducted from the scales. Thus for each fish, known to have been tagged, there remained a restricted list of possible tag numbers. In some cases this list was rather large, the largest containing 43 possbilities.

Of the 34 tags recovered intact on fish in the gill net fishery, 32 were accompanied with readable scales from the fish they represented. These sets (one from the fish when tagged, the other from the fish when recovered) were compared by projecting the images at 100 diameters' magnification and counting circuli for each growth year. Of the 113 growth years which could be compared, circuli counts exactly agreed on but 23. Differences were as follows: 43 off 1, 22 off 2, 13 off 3, 7 off 4, 1 off 5, 1 off 6, 2 off 7, and 1 off 8. The greatest differences appeared associated with the third growth year, the best agreement was found in the region of fresh water growth. Thus circuli counts or a count formula

TABLE II. Comparison of lengths recorded for live fish when tagged and for the same fish when landed in the gill net catch.

Difference at recapture	Frequency
inches	
+1.5	1
+1.0	0
+0.5	9
0	20
−0.5	4
−1.0	0
Total	34

(i.e., 11(I), 5+21(II), 23(III), 22(IV), 23(V)) for a particular scale were only useful in a gross sense for eliminating possible solutions of an unknown. Measurements of proportion along the anterior radius also proved to be of limited value. Both the size of the scale and proportional parts were found to vary between scales from the preferred areas of the same fish. To complete this analysis the more subjective method of comparing photographs of scales in question was used. Features such as zones of irregular formation or of fast growth provided clues as to the most probable solution. The results of this "scale matching" procedure are as follows:

1. The actual gill-net catch of troll-tagged chinook was 34 (complete tag affixed) + 2 (incomplete tag affixed) + 14 (tag lost), or 50 fish.
2. The apparent tag recovery was 34 (complete tag affixed) + 2 (incomplete tag affixed) + 10 (tags but no fish), or 46 fish.
3. Five of the above 10 tags came from fish landed, 4 from fish landed by the same fisherman that recovered the tag, 1 from a different fisherman. The remaining 5 tags were from fish which either died from their encounter with the net or recovered and formed part of the spawning escapement.
4. For 9 of the 14 troll-marked fish, the tags were permanently lost.

The struggling of the fish in the nets which led to loss of tags may have resulted in the death of the 5 fish above for which no further information is available. In this case a distinction must be made between fishing mortality and catch, the former being the larger figure. With this assumption, fishing mortality may have been $34 + 2 + 14 + 5 = 55$. Thus the apparent tag recovery would be in error as a measure of gill net fishing mortality. A maximum correction coefficient of 1.196 is indicated.

DISCUSSION

While the number of tags reported in this experiment is small, it indicates a source of error which could seriously affect estimates of population size and fishing mortality. While 23 fish were recovered from non-Taku areas, no knowledge of relative fishing intensities is available with which to weight these catches and calculate the portion of the tagged stock available to the trollers which was composed of maturing Taku River fish. For the sake of a realistic example, however, it is assumed that 377 or $\frac{2}{3}$ of the 555 fish tagged were maturing Taku River stock. This figure should be corrected for tagging mortality, which is unknown. From independent studies (Parker and Black, 1959) this error may have been about 70%. Thus an estimated 113 tagged fish were available to the Taku River gill net fishery. On this basis the apparent tag recovery of 46 fish would lead to an estimate of fishing mortality rate of 46/113 or 0.407, during the chinook season. This is, however, an underestimate as the actual catch of tagged fish was shown to be 50 fish, thus fishing mortality rate is estimated as 0.442. Again this is probably an underestimate as the fishing mortality of tagged fish may have been as high as 55, thus the maximum estimate of fishing mortality rate is 0.487. A 20% error may be ascribed to failure of the tags in a gill-net fishery, leading to an underestimate of fishing mortality.

The applicability of these results to other tagging experiments may be questioned, and it is not my intention to provide a numerical correction factor. Petersen tags affixed at the origin of the dorsal fin have also been returned in significant numbers after being found in the nets or in the bilge of the fishing boat. Thus the present experiment indicates a source of error which may seriously affect estimates of vital statistics if the researcher is not cognizant of its existence.

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Dogfish Gelatin[1]

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ABSTRACT

Gelatin has been prepared from the skin and skeleton (separately) of the dogfish, *Squalus suckleyi*. The gelling and melting points of a 10% solution were 15 and 22°C respectively, for gelatin from skin, and 14 and 23°C for that from skeleton. The skin gelatin contained 16.3% total nitrogen, 6.4% hydroxyproline, and 0.28% tyrosine. The corresponding values for skeleton gelatin were 15.7, 8.8, and 0.29%. Yields of gelatin were low, being 7% from skin and 2% from skeleton on a wet-weight basis.

INTRODUCTION

The problem of the utilization of the Pacific coast dogfish (*Squalus suckleyi*) has been considered in detail by Tarr (1958), and efforts have been made in this laboratory to try to improve means of utilizing this fish (Moyer *et al.*, 1959) or to find other uses for it. Although its use in the manufacture of gelatin or glue has been considered in the past, little information on the subject is available in the literature. An unsuccessful attempt to prepare glue from the whole carcass was made by Smith (1931). Takahashi and Tanaka (1953) demonstrated the skin has a very low shrinkage temperature, and Takahashi and Yokoyama (1954) reported that on a dry-weight basis it contains 36% placoid scales and yields 22% ash. Similar investigations of other species of dogfish indicated the skin of *S. acanthias* is unsuitable for glue manufacture, in part at least because of the black pigment it contains (Alexander, 1923), and the collagen of the placoid scales of *Mustelus canis* (and of some other elasmobranch fishes) was found to be extractable only by very prolonged boiling, after which procedure the extract would not gel (Green and Tower, 1901).

The present report describes the results of an investigation into the possibility of preparing gelatin from both the skin and skeleton of the Pacific coast dogfish.

MATERIALS AND METHODS

Dogfish freshly caught were either used at once or were frozen and stored at −28°C until needed. The fish were washed thoroughly with tap water before they were skinned.

Dry weights of skin and skeleton were determined after drying to constant weight at 105°C. Ashing of skin and skeleton, and determination of calcium and

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phosphorus in the ash were carried out by the methods of the Association of Official Agricultural Chemists (1945).

The gelling and melting points of gelatin solutions were determined by pipetting 5 ml of solution into an 18 × 150-mm test tube then placing the tube in a water bath the temperature of which could be gradually varied. The gelling point was that temperature at which the gel set, and the melting point that at which the gel was observed to break down when the tube was tipped on its side.

Total nitrogen was measured by micro-Kjeldahl procedure and chloride by the Mohr method.

Hydroxyproline was estimated by the method of Neuman and Logan (1950) as modified by Leach (1960), and tyrosine by the procedure of Bernhardt (1938).

EXPERIMENTAL

Examination of six dogfish, each of which weighed about 2 kg, showed that the skin accounted for 8% (range 7.5 to 9.3%) and the skeleton for some 15% (range 9.8 to 19.7%) of the whole body weight. Spines and fin rays were included with the skeleton. The wide range in weights of skeletons was the result of variations in the extent to which these were freed from extraneous matter. It is improbable that under commercial conditions it would be possible to clean skeletons as completely as they were cleaned in this work. The dry weights of skin and skeleton were found to be 26 and 20% of their wet weights, respectively. On these dry-weight bases, the skin and skeleton yielded 19 and 21% ash, respectively. Calcium accounted for 48% and phosphorus for 18% of the ash of skin, while the corresponding values for the ash of skeleton were 37 and 16%.

The influence of several different pretreatments of skin and skeleton, and of various temperatures and periods of extraction, on the yield and quality of gelatin was investigated. The pretreatments to which the skin and skeleton (previously cut into small pieces) were separately subjected, were as follows:

(A). Washing in running tap water at 7°C for 24 hours.

(B). Extraction at 20°C over a period of 24 hours with five changes of a 10% (w/v) solution of sodium chloride, followed by 4 hours of washing in cold running tap water.

(C). Treatment as in (A) above, followed by extraction at 20°C over a period of 24 hours with two changes of a 0.2% sodium hydroxide solution then by 15 minutes washing in running tap water. This was followed by a further extraction with two changes of 0.2% sulphurous acid solution at the same temperature and for the same period of time as for the alkali treatment, and finally by a further 4 hours washing in running tap water.

(D). Treatment as in (B) above, followed by extraction at 20°C over a 24-hour period with two changes of 0.1 *N* hydrochloric acid, and finally by washing for 4 hours in running tap water.

Gelatin was extracted from samples pretreated as above by heating them in 200 ml of water for each 100 g of pretreated material, the extraction being

repeated as required. Extraction temperatures investigated ranged between 50 and 107°C, while extraction periods ranged from 30 minutes to 4 hours. Extracts were clarified while warm by centrifugation at 10,000 g and were concentrated either by evaporation under reduced pressure at 55°C or by lyophilization before any analytical procedures were applied. The results may be summarized briefly as follows:

Gels with the highest melting point (22 to 24°C for 10% solutions) were prepared with gelatin extracted at temperatures of 70 to 80°C for two consecutive 30-minute periods from material pretreated by procedure (C). Extraction at 100°C for a period as short as 30 minutes resulted in a lowering of the gel melting point by 2 to 5 degrees C in comparison with extraction at 70 to 80°C. Two consecutive ½-hour extractions with water at 70 to 80°C appeared to be adequate, a third extraction with water bringing little additional gelatin into solution. Typical yields of gelatin were 7 and 2% of the wet weight of the skin and skeleton, respectively. Further extraction with 1% acetic acid at 70°C for two 1-hour periods of the residue remaining after the second water extraction at 70°C of material pretreated by procedure (C) brought into solution an additional 1.8% and 1.5% of the original wet weight of the skin and skeleton, respectively. Of the residue remaining after these extractions, 96% of the dry weight of that from the skin and 42% of that from the skeleton were soluble in 200 volumes of 40% urea at 100°C in 24 hours. Gels prepared from the material extracted with acetic acid had a very low melting point. The material soluble in urea has not been further investigated but is presumably difficultly extractable or degraded collagen and elastic tissue (Hall, 1955). Higher yields of gelatin of the order of 10% of the wet weight of skin and skeleton were obtained by extraction of the pretreated material at higher temperatures (100 to 107°C) but, as pointed out above, the gelling properties of such extracts were poor; in fact, in some instances, they failed to gel. Attempts to increase the yield from skeleton by grinding the pretreated material before extraction did not materially increase the yield of gelatin and resulted in the suspension of a large amount of very finely dispersed insoluble matter that was difficult to remove from the extract.

Table I presents typical data for gelatins extracted from dogfish skin and skeleton under the conditions we have found to be most favourable. These conditions are closely similar to those found suitable for preparation of gelatin from fish skins, and patented by Kernot (1924).

The gelatin from both skin and skeleton was nearly colourless and had only a slight odour. It was found that although the skin of *S. suckleyi*, like that of *S. acanthias* (Alexander, 1923), contains black pigment, this may be removed by squeezing the skin during pretreatment.

DISCUSSION

The yields of gelatin obtained in the present work were low, and it appears unlikely that they could be improved greatly without serious impairment of the gelling properties of the product. Yields of gelatin from the skin of Pacific

TABLE I. Gelatin from skin and skeleton of dogfish (*Squalus suckleyi*).

	Percentage of dry weight of gelatin*	
	From skin	From skeleton
Total nitrogen	16.3	15.7
Chloride	0.46	0.45
Hydroxyproline	6.4	8.8
Tyrosine	0.28	0.29
Melting point†	°C	°C
of 2% solution	18	19
of 10% solution	22	23
Gelling point§		
of 2% solution	7	8
of 10% solution	15	14

*Prepared by two consecutive 30-min extractions at 70°C from material pretreated by method (C). Yields, 7% from skin and 2% from skeleton based on wet weight of fresh material.

†Extracts concentrated by lyophilization for preparation of 2% and 10% (w/v) solutions.

§The gelling points of 2 and 10% solutions (w/v) of a purified calfskin gelatin (Eastman) determined in this fashion were 16 and 26°C respectively, while the corresponding melting points were 26 and 29°C.

dogfish do not appear to have been recorded previously, but Takahashi and Yokoyama (1954) have reported a yield of 12% from the skin of the great blue shark, *Prionace glaucus*. This yield appears to have been obtained by the use of rather drastic extraction procedures (five extractions at 100°C with six volumes of 5% acetic acid) and no data regarding the gelling properties of the product were provided. Yields approaching those reported by Takahashi and Yokoyama were obtained in the present work, but only by extraction procedures that impaired the gelling properties of the product. The water content of the dogfish skin was similar to that found for skin of other sharks (Takahashi and Shiokawa, 1953) and of cod (Young and Lorjmer, 1960), but the ash on combustion was nearly double that found for whole cod skin (Young and Lorimer, 1960). Comparable data for yield of gelatin from skeleton of other elasmobranch fishes do not appear to be available, but fish bone has been said to yield little glue or gelatin (Kernot and Speer, 1926) and yields of glue from fish heads have been reported to vary between 3 to 4.5% (Tressler and Lemon, 1951) and to be as high as 14% (A. Guttmann, personal communication, 1961).

The melting and gelling points of dogfish gelatin are lower than those that have been reported for gelatin from the skin of an unstated species of shark (29.5 and 23.3°C, respectively, Kikuti, 1939), and for gelatins from mammalian hides. These differences may be related to the low shrinkage temperature of dogfish skin (34.5 to 38.7°C) compared to that (52 to 53.5°C) of other sharks (Takahashi and Tanaka, 1953) and mammals (e.g., 65°C for calf skin, Gustavson,

1954), for there is evidence that the stability of collagens is directly related to the shrinkage temperature of the skins from which they are prepared (Gustavson, 1942).

The hydroxyproline content of dogfish-skin gelatin is similar to that reported for the collagen of cod skin (Young and Lorimer, 1960; Gustavson, 1954), a skin that also has a low shrinkage temperature (40°C), but somewhat less than the hydroxyproline content of gelatins from the skins of certain other sharks and fish (Eastoe, 1957; Piez and Gross, 1960). The hydroxyproline content of the dogfish skeleton gelatin was similar to that of cod-bone gelatin (Eastoe, 1957; Piez and Gross, 1960), but was higher than that found for elastoidin gelatin from *S. acanthias* and lower than that for elastoidin gelatin from other sharks (Gross and Dumsha, 1958).

The tyrosine content of the dogfish-skin gelatin was very low, similar to that reported for gelatin from other sharks and fish (Eastoe, 1957; Piez and Gross, 1960). That of the skeleton gelatin was also low, as for cod-bone gelatin (Eastoe, 1957), but much lower than that for elastoidin gelatin from *S. acanthias* and other sharks (Gross and Dumsha, 1958; Piez and Gross, 1959).

The nitrogen content of the dogfish gelatins is lower than that found for shark skin gelatin (16.9%) by Kikuti (1939) and those (17.5 to 18.5%) usually reported for gelatins or collagens (cf. Gustavson, 1954; Young and Lorimer, 1960; Veis and Cohen, 1955). This may possibly be related in part to the mild extraction conditions and low yield in the present work, for Veis and Cohen (1955) have reported values as low as 16 to 17% nitrogen for gelatin prepared by only partial extraction under mild conditions.

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Olfactory Perception in Juvenile Salmon.
I. Observations on Response of Juvenile Sockeye to Extracts of Foods[1]

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ABSTRACT

The introduction of aqueous extracts of natural foods into an aquarium holding juvenile sockeye evoked exploratory and feeding responses in fish that had previously eaten the foods, but failed to do so in fish that had not. Responses were characterized by breaking up of the school, increased swimming speeds, and the swimming of the fish into lighted areas. The fish detected concentrations of the active substance(s) in the order of one part in 80,000,000, based on the wet weight of the whole food.

INTRODUCTION

The ability of several species of fish to detect food by odour has been well documented (e.g. Parker, 1910; Steven, 1959; Hasler, 1954), and certain compounds present in foods have been shown to be capable of eliciting feeding behaviour in fish (Steven, 1959). However, the minimum concentration of these compounds required to induce the response appeared to be very much greater than that which could possibly have been present in aqueous extracts of foods that were equally effective (Steven, 1959), and was certainly very much higher than the concentrations of certain organic compounds that have been shown to be detectable by odour by various species of fish (see review by Hasler, 1957). It thus appears probable that the compounds which actually attract fish to food by odour are as yet unidentified, although a few of their properties have been examined (Tester *et al.*, 1955; Steven, 1959). In view of this, we have undertaken a study of odour perception of food by sockeye salmon (*Oncorhynchus nerka*). Sockeye smolts have been used in this work primarily because they can be more readily obtained and maintained in an aquarium than the adult fish, but eventually it is intended to extend the work to include adults.

The present report records observations on the response of smolts to aqueous extracts of marine organisms that are either known to contribute to the diet of the adult fish at sea (International Pacific Salmon Fisheries Commission, 1956; Allen and Aron, 1958) or to be available to them in their marine habitat.

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METHODS AND MATERIALS

Sockeye smolts (*O. nerka*) were obtained during March 1960 from traps located at the outlet of Great Central Lake. This water system, located in the Alberni area of Vancouver Island, B.C., supports a well-established population of sockeye. Approximately one thousand smolts were procured over a 24-hr period.

The transport tank used to transfer the fish from the field site to the Vancouver Public Aquarium was a 400-gal circular insulated aluminum tank 4 feet in diameter and 4 feet in height mounted on a truck. Continuous water circulation was maintained during transport at the rate of 3 gal/min through the use of a bilge pump, and in addition the water was aerated with oxygen supplied by a pressure cylinder. The temperature of the water in the transport tank increased from 7°C at the field site to 9°C upon arrival at the Vancouver Public Aquarium 5 hours later. The fish were held at the Aquarium in $6 \times 3 \times 3$-foot cement tanks supplied with a continual flow of water, until February 1961 when they were transferred to the laboratory and placed in oblong $4 \times 2 \times 2$-foot fibreglass tanks. The water inlets in the fibreglass tanks were placed so as to create a slow current. All water used was first dechlorinated. To minimize the possibility of the fish becoming conditioned to light, all holding tanks were covered with black plastic covers.

The smolts were maintained in good health on a diet of Clark's fish pellets (J. R. Clark Co., Salt Lake City, Utah), supplemented twice weekly with a meat ration consisting of 55% canned salmon, 20% beef liver, 20% beef heart, 5% pablum and a tablespoonful of iodized salt for every 10 lb of feed. By the beginning of February 1961, when this study was initiated, the fork lengths of the fish varied between 115 and 147 mm.

Zooplankton were netted at various points in Burrard Inlet and the Strait of Georgia, B.C. Brine shrimp were a frozen commercial product.

Experiments were carried out in an area from which extraneous noise, light and movement were eliminated. The bioassay method used to assess the attractiveness of various aqueous extracts of foods and commercial bait oils for juvenile sockeye was patterned closely after that of Steven (1959). One modification of Steven's system was made, however, in order to take advantage of the photonegative behaviour of sockeye smolts (Hoar, 1958). The end quarter opposite the water inlet of each aquarium was darkened by a black plastic sheet which extended across the top and down the side of each tank. The remaining three-quarters of the tank was illuminated by a single 300-watt photoflood lamp placed 18 inches from the exposed end of the tank. Only on very rare occasions apart from experimentation periods were sockeye observed to be present in the lighted area of the tanks. The arrangement of the two identical glass aquaria used (each $5 \times 2 \times 2$ feet) is shown in Fig. 1 and 2. The serum bottles used to hold the test or control solutions were fitted with fine-bore stopcocks and the system was arranged to deliver between 80 and 85 ml to each aquarium through the water supply inlet in 60 sec. All extracts tested were introduced into aquaria

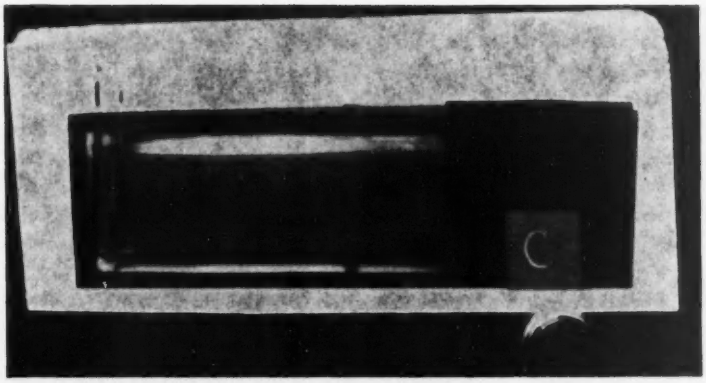

FIG. 1. Enlargement from a frame of 16-mm ciné film taken during the testing of the effect of a 1% aqueous zooplankton extract on juvenile sockeye conditioned to this food. Black area to right is cover down side of aquarium which also extends across the top of the tank. This frame was taken from control portion of film made before injection of test extract.

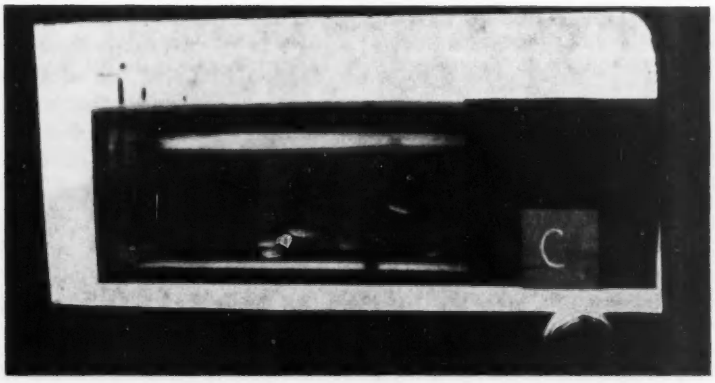

FIG. 2. Enlargement from another frame of same ciné film used in preparing Fig. 1. This frame was taken 4 min 40 sec after completion of injection of test extract.

in 250-ml aliquots. The bioassay system was checked continually during test periods to insure minimum variations in illumination, water flow and sample delivery rates between the two tanks.

Tests with potassium permanganate showed that the time interval for distribution of the compound throughout the whole of each tank varied from 2 min 14 sec to 2 min 55 sec from the time of injection. It required between 4 hr 20 min and 4 hr 45 min to clear all visible traces of permanganate from each tank. The variation in timing reflects the small changes which occur in the water delivery rates. No back flow into the sample bottles was noted during the distribution tests.

The portion of the room containing the two experimental tanks was partitioned off with black plastic curtain extending from the floor to the ceiling and running in a semicircle around each aquarium. A peephole large enough to accommodate a camera lens was cut into the curtain at a point directly opposite the centre of each tank. The distance from the centre of the outer glass side of the tank to the camera was 6 ft. The curtain enabled the investigator to record the responses of the fish with a 16-mm ciné camera without being seen by them. One additional peephole was provided for each tank by mounting a 4-inch square piece of transparent mirror in the end plywood partition 10 inches above the water level of each tank.

The aqueous extracts of the various foods tested were prepared by grinding samples and then suspending weighed amounts in a known volume of distilled water. The suspension was thoroughly mixed for 10 to 20 min and then filtered through Whatman No. 1 filter paper. Preparation and storage of extracts before testing was carried out at 5°C. All the aqueous extracts tested were colourless and only the squid extracts had any detectable odour to the experimenter. Certain commercial bait oils also tested were dispersed at the desired concentration in distilled water.

The responses of the fish to the aqueous extracts of the food were studied by introducing 250-ml aliquots of each sample into one aquarium via the water supply while an equal amount of distilled water was injected by the same manner into the other aquarium. As the fish normally congregated behind the black plastic curtain (*vide supra*), any change in behaviour leading to their movement into the open was readily observed. The behaviour pattern of the fish was watched for 10 min before and 20 min after the completion of each injection. If a response was obtained, it usually occurred 2 to 4 min after the start of the injection. A 24-hr period was allowed between successive tests. Each of the serum bottles was washed exhaustively with dechlorinated water and dried before the next test. All extracts were tested in duplicate, the school in each tank being used in turn as control for the other. All extracts evoking a positive response were tested several times with different schools of sockeye. The tests were carried out either in the early forenoon or early afternoon before the fish received their daily feeding.

A sample was said to elicit a positive "exploratory" response when (1) the school dispersed; (2) the fish left the shaded area and entered the lighted portion of the tank; (3) the swimming speed of the fish increased. In certain instances the fish in addition sampled objects on the bottom of the tank or broke through the surface of the water in chase of some small object floating on the water surface. This behaviour was termed a positive "feeding" response. In every case where feeding behaviour was evoked, an exploratory response was also evident.

Pilot experiments indicated that from 6 to 12 fish in each aquarium was an adequate number for visual observation and to provide a consistent response. Larger numbers of fish in each tank tended to produce an overcrowding effect and at times made the interpretation of behaviour questionable. In view of these considerations, 10 fish were held in each tank during testing periods. To

minimize conditioned responses, schools were discarded and replaced with fresh ones after each series of experiments, or at the end of 3 weeks, whichever came first. To determine the effect of the introduction of test samples on the temperature and pH of the aquaria water, 250-ml aliquots of distilled water, 1% zooplankton, and 1% brine shrimp aqueous extracts were introduced into the aquaria in the usual manner. No apparent differences in the pH or temperature of the aquaria water were detected immediately following the completion of the introduction of these samples.

RESULTS

Presently available information (International Pacific Salmon Fisheries Commission, 1956) indicates that adult sockeye are plankton feeders in their natural habitat. As zooplankton are difficult to obtain in uncontaminated form and as the supply is uncertain during the winter months, several foods in addition to zooplankton were tested initially to determine their ability to evoke exploratory and feeding behaviour in the juvenile sockeye. The extracts tested and the responses obtained are shown in Table I.

TABLE I. Response of juvenile sockeye to aqueous extracts of several foods.

Food	Concentration of extracts	Number of tests	Response	
			Exploratory	Feeding
	gram %			
Beef liver	1.0	2	+	+
Beef liver	0.1	2	+	+
Beef heart	1.0	4	+	+
Beef heart	0.1	2	+	+
Zooplankton	1.0	6	–	–
Zooplankton	0.1	4	–	–
Brine shrimp	1.0	4	–	–
Brine shrimp	0.1	2	–	–
B.C. shrimp	1.0	2	–	–
B.C. shrimp	0.1	3	–	–
Squid	1.0	4	–	–
Squid	0.1	2	–	–

It is apparent that exploratory and feeding behaviour was evoked only by aqueous extracts of foods to which the fish had presumably been previously conditioned through eating, in this case beef liver and beef heart. The fish had not eaten the substances to which they failed to respond; two of these, squid and marine zooplankton, are known major constituents of the natural diet of adult sockeye. Brine shrimp are not known to exist off the British Columbia coast or to contribute to the diet of sockeye homing in this area, but are abundant along the California coast (Bond, 1959) and conceivably could constitute part of the diet of those races of sockeye frequenting the latter area. Ricker (1937) reported that pelagic plankton crustaceans formed practically the only food of

sockeye fingerlings in Cultus Lake, insects being rarely taken. Since it appeared that the smolts were responding only to extracts of those foods to which they had been conditioned by previous eating, an attempt was made to condition two groups of smolts, one to zooplankton and the other to brine shrimp. Conditioning was carried out by adding small amounts of the substance to the meat supplement for one week followed by daily dispersal of small amounts of the food on the water surface of the tank. It was found that the fish usually became conditioned (see below) by the middle of the second week of feeding. The responses of conditioned fish to serial dilutions of zooplankton and brine-shrimp aqueous extracts are given in Table II and III.

TABLE II. Response of conditioned juvenile sockeye to aqueous extracts of brine shrimp.

Concentration of extracts	Number of tests	Response	
		Exploratory	Feeding
gram %			
1.0	2	+	+
0.1	2	+	+
0.01	2	+	+
0.005	2	+	+
0.0025	2	+	+
0.0010	4	+	+
0.0004	2	+	–
0.0002	2	+	–
0.00013	4	+	–
0.00010	2	–	–

TABLE III. Response of juvenile sockeye conditioned to whole zooplankton when offered aqueous extracts of zooplankton.

Concentration of extracts	Number of tests	Response	
		Exploratory	Feeding
gram %			
1.0	2	+	+
0.1	6	+	+
0.01	2	+	+
0.001	6	+	+
0.0004	4	+	–
0.0001*	4	?	–

*Trace response obtained in 3 out of 4 tests.

It is apparent that once the fish had been conditioned by eating either brine shrimp or zooplankton, aqueous extracts of these organisms evoked both exploratory and feeding responses in the appropriately conditioned fish. Although not recorded in the Tables, it was found that fish conditioned to zooplankton but not to brine shrimp did not respond to the extract of the latter, and vice versa.

Numerous commercial bait attractants and countless home recipes for attractants are readily available to the sport fisherman (Johnson and Johnson, 1956). Generally, the attractant is an oil or a mixture with an oil base and is used as a bait dip. While few of the commercial attractants are promoted as attractants for specific fish, several have been advanced as attractants for a wide variety of fish including trout and salmon. Since considerable support exists for these commercial and home-prepared bait attractants, several were selected to determine their effect on the behaviour of juvenile sockeye. For testing, the oils were suspended in 250 ml distilled water and an equal volume of distilled water was used for the control.

Of the five commercial bait oils tested, only menhaden oil produced an apparent change in the behaviour of the fish (Table IV). The response to this

TABLE IV. Response of juvenile sockeye to commercial bait oils.

Oil	Concentration of suspension	Number of tests	Response	
			Exploratory	Feeding
	gram %			
Cumin	0.04	2	–	–
Cumin	0.40	2	–	–
Fish liver oil	0.04	2	–	–
Fish liver oil	0.40	2	–	–
Patchouli	0.04	2	–	–
Patchouli	0.40	2	–	–
Anise	0.04	2	–	–
Anise	0.40	2	–	–
Menhaden	0.04	2	+	–
Menhaden	0.40	2	+	–

oil, while consistent at both concentrations tested, was weak in that not all the fish responded. It was characterized by a breaking away of 3 to 4 fish from the school, and by rapid spurts of swimming for short periods of time.

DISCUSSION

Steven (1959) reported that both silversides (*Hepsitia stipes*) and tomtates (*Bathystoma rimator*) displayed exploratory feeding when exposed to dilute seawater extracts of a number of foods. Some of these foods, such as plankton, formed part of the diet of the fish before capture, and others, such as beef liver and clam, were fed to them during captivity. Beef muscle and cod muscle, however, were not fed and would not form part of their diet in nature, yet dilute extracts of these muscles evoked exploratory responses.

The sockeye smolts with which we have worked did not respond to any of the food extracts tested except when they had previously eaten the foods, but they did show some response to menhaden oil, although this oil had not formed part of their diet. Other fish oils and meals (but not liver oils) were contained in the pellets with which they were fed (personal communication, J. E. Hanson,

Fisheries Biologist, J. R. Clark Co., Salt Lake City, Utah). It is clear that in the present work the fish became conditioned to some component(s) of their foods but there is some evidence that they may be attracted by extracts of foods that they have not previously ingested. This appears also in the results of Steven (1959) and Tester *et al.*, (1955). The reason for this response is not known but perhaps some cross-conditioning between different foods may occur, particularly when relatively high concentrations of extracts are used.

It appears that sockeye, like other fish (Hasler, 1957), have a very keen sense of smell, as evidenced by their ready response to the introduction into a 200-litre aquarium of an extract equivalent to 2.5 mg wet weight of either brine shrimp or zooplankton.

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Photographing Halibut Otoliths for Measuring Growth Zones[1]

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ABSTRACT

Apparatus is described for clearing, projecting and photographing halibut otoliths for use in growth studies.

Pacific halibut otoliths are photographed by reflected light on 35-mm film strips. These strips are then projected in a slide projector to a table top screen and measurements are made from the enlarged image.

Otoliths to be photographed are cleared and stored in a solution of 50% glycerin and water to which a small amount of thymol for preservation has been added. This solution clears the otolith in approximately two weeks. Cleared otoliths are placed in a blackened petri dish to which has been affixed a 1-centimeter mark from a metric scale and a blank white rectangle (Fig. 2, below). The centimeter mark provides an easy and positive means of determining the magnification of each frame when it is projected; the blank rectangle provides a space to write the identifying otolith number on the film after it has been processed. The cleared otolith is placed in the petri dish between the centimeter mark and the rectangle and covered with a clean solution of glycerin and water prior to being photographed.

Two cameras have been used. First an Exakta VX with a 50 mm Tessar lens, and at present a Leica IF on a focus-slide with a 35 mm Summaron lens. Extension tubes are used with both cameras to secure sufficient magnification: in this case magnification is great enough so that the otolith image, the centimeter mark and the blank rectangle fill the frame. To reduce the number of camera and projector adjustments, the amount of magnification has been determined from the largest otolith in the sample. The camera is fixed in this position and not moved for smaller otoliths.

The camera is mounted on a rigid stand in a vertical position. Gross focusing is accomplished by moving the camera along the vertical rod of the stand. Fine focusing is accomplished by focusing the lens in the usual manner. Accuracy of focusing is checked by examining the ground glass image with a low power magnifying glass.

Otoliths are illuminated by reflected light, provided by a 100-watt Bausch and Lomb microscope light, which has been diffused through a sheet of ground glass. The distance from the otolith to the lens of the light is approximately 13 cm. The incidence angle is approximately 45°. However, this angle does not appear to be important and is obscured due to the diffusion of the light.

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Comparable exposures have been obtained over a considerable range of incidence angles.

Eastman Kodak Panatomic-X film, rated at 80 ASA, is reversed chemically to produce a positive image. The film speed number has little meaning in this situation unless an extremely sensitive light meter is available and should be interpreted as a guide number only. The film is processed with an Eastman Kodak Direct Positive Film Development Kit. An exposure of 1/100 second at f 8 is used in photographing halibut otoliths. However, the proper exposure must be determined for each situation depending upon the intensity of illumination, the amount of contrast desired, and the amount of magnification. The degree of contrast can be controlled with the first development.

Modified development procedures have been worked out, as follows:

Developer — first	8 minutes	Rinse in water	30 seconds
Rinse in water	30 seconds	Acid fixer	5 minutes
Bleaching bath	3 minutes	Rinse in water	30 seconds
Clearing bath	2 minutes	Acid fixer eliminator	3 minutes
Developer — second	8 minutes	Wash in running water	30 minutes

The inherent color in the base of the Panatomic-X film reduces the flare of the highlight areas when the image is projected onto a white screen. Resolution of Panatomic-X film is approximately that of the direct positive film and has proven satisfactory for this purpose.

Standard 36-exposure rolls of film are used. One frame is used for identification purposes, 35 frames for photographing otoliths.

The film strips are projected with a 35 mm American Optical film strip projector Educator model using a 3-inch lens from a projection stand onto a white table-top screen: a 20 × 25 inch cellulose acetate sheet. A front-surfaced mirror is placed at 45° to the horizontal projection path to deflect the image onto the table-top screen.

Figure 1 shows the projection equipment in use. The projection stand, made of stainless steel, is approximately 27 inches (69 cm) high (A). The upper extension (B), which holds the front-surfaced mirror, is about 24 inches (61 cm), the lower (C) is about 38 inches (96 cm). These measurements allow a 5-foot (152 cm) projection distance (D) needed to obtain sufficient magnification and still leave controls (E) of the projector within reach of the operator when seated at the table. Slotted extension arms and wing nuts (F) provide minor control of the angle of the mirror. The projector is mounted in a slotted track (G) and can be moved back and forth to change the projection distance.

The lens housing and film strip holder of the projector can be rotated 360°. This movement allows checking the effective parallelism of the film plane and the screen by placing the centimeter mark on each side of the projected frame. Controls on the mirror permit adjustments so that the desired magnification is obtained on each side of the frame thereby assuring that the film plane and screen are effectively parallel.

Measurements of the radii of annual growth zones from the nucleus to the end of the winter zone are made in millimeters on the projected positive image which has been enlarged 20 times.

This technique of photographing and measuring halibut otoliths has proven satisfactory. The centimeter mark and an otolith are shown in Fig. 2. It is possible to photograph and process the films for approximately 200 otoliths in a day. Measurements of each growth zone have been made on approxmately 120 otoliths per day where the average number of zones per otoliths is near 12.

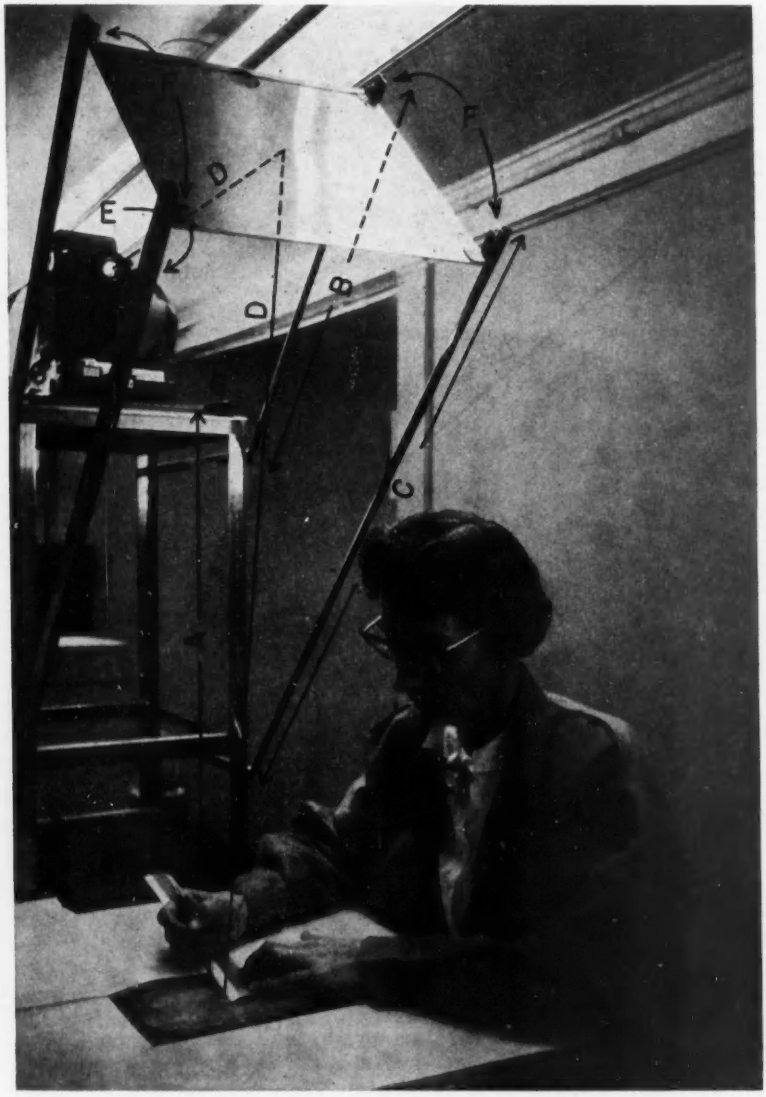

FIG. 1. Photograph of the projection stand. Inked letters refer to dimensions of the stand as described in the text.

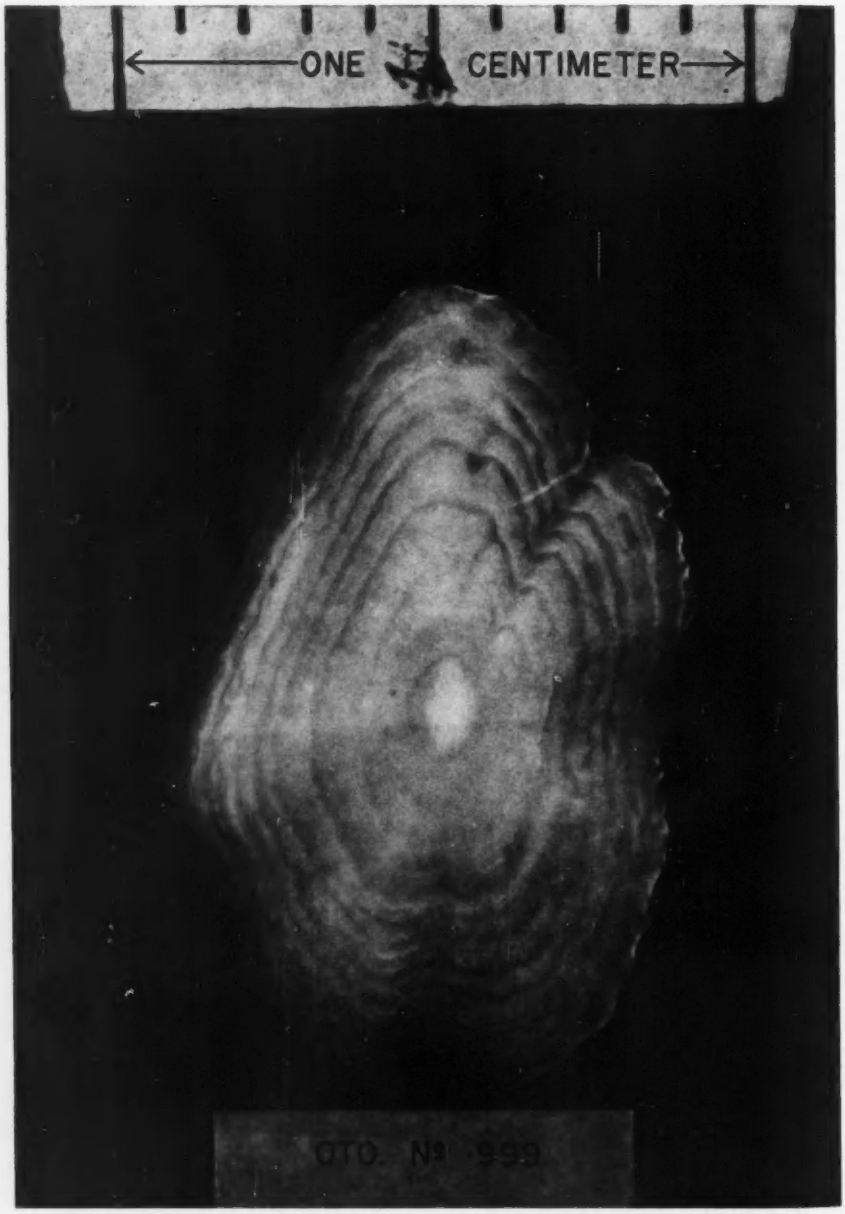

FIG. 2. Photograph of Pacific halibut otolith, centimeter mark and white rectangle with identification number.

A Method of Calculating Body Lengths from Otolith Measurements for Pacific Halibut and its Application to Portlock-Albatross Grounds Data between 1935 and 1957[1]

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ABSTRACT

A change in growth rate of the halibut from the Portlock-Albatross grounds has occurred since the early 1930's. It is possible to measure this change in growth by studying the otoliths of fish taken by the commercial fishery in subsequent years. The calculation of body lengths from otolith measurements has provided a technique of reconstructing the growth patterns of each year-class. This method has been tested using the otoliths of recovered tagged halibut. The percentage deviations from average body length at each age demonstrate an increase in average length with time over the period 1920–1956. This increase is not exhibited among young fish of ages 1 through 4; it starts approximately with age 5 and continues throughout the older ages, where it is pronounced.

INTRODUCTION

Under the existing 1953 Convention, the International Pacific Halibut Commission is responsible for preserving the Pacific halibut fishery, developing the halibut stocks to levels which will permit maximum sustainable yields and maintaining the stocks at those levels. These objectives expand the responsibilities of the preceding treaties and require more detailed knowledge of the complex biological principles that govern the size of a population of living organisms. The weight of a halibut population available to the fishery depends

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upon the number of young produced each year, their growth rate and their mortality rate. The first two increase the size of the stock while the latter decreases it. To effectively manage a stock of fish at high levels of population density reliable measures of these rates must be known. It is the purpose of this paper to describe a method of calculating lengths at successive annuli directly from a regression formula without any adjustment for the observed size of the individual fish. It will be shown that this method gives good average results, sufficient for the intended purposes. This method is applied to data from market samples of the commercial fishery.

The calculation of body lengths from scale measurements has been used extensively in many fishery investigations. Lea (1910), working with herring, used a linear relationship between scale measurements and body length. Fraser (1916, 1917) computed the lengths of salmon from scale measurements using a linear relationship plus a correction factor for the length of the fish when the scale was formed. Sheriff (1922), working with herring, discusses a parabolic relationship between scale measurements and body length. Van Oosten (1929), working with lake herring, applied Lea's scale formula. Hile (1940), working with cisco, refers to Van Oosten's application of the scale method of calculating lengths at earlier ages as do many workers studying the life histories of freshwater fishes in the midwestern regions of the United States. Seatersdal (1953) discusses growth calculations based on a curvilinear relationship between otolith size and fish length of haddock in Norwegian waters. He also refers to Graham (1929) and Menon (1950) who have reviewed or listed much of the literature available on the method of calculating lengths from scales or otoliths.

Development of a method of calculating lengths at each age from the measurements of the growth zones of halibut otoliths will furnish estimates of the growth rate at a comparable time in each growing season for the commercial and sub-commercial ages from year to year. Such a method also permits estimation of the length of halibut in the year classes between the sampling by tagging operations in the middle 1920's and the start of the "market sampling" program of the Commission's staff in 1935.

The method of calculating lengths at earlier ages depends upon the accuracy of the age determinations. Dunlop (MS, 1961) has shown, with a large sample of otoliths taken throughout the range of the fishery at monthly intervals, that not more than one annulus is formed each year. The growth of the opaque band begins approximately the end of April and continues until about the following October. The growth of the hyaline band extends from approximately October to April. Good agreement is obtained between successive readings of a sample by an individual or between single readings of a sample by two individuals. Most of the disagreements amount to only one year and occur generally in the older ages.

An increase in growth rate of halibut has been evident in the Area 3 populations since the middle 1930's. This increase in growth rate is shown by comparison of the weights of female halibut at the same ages in the samples from Portlock grounds and Shumagin Islands grounds (Fig. 1, Table I).

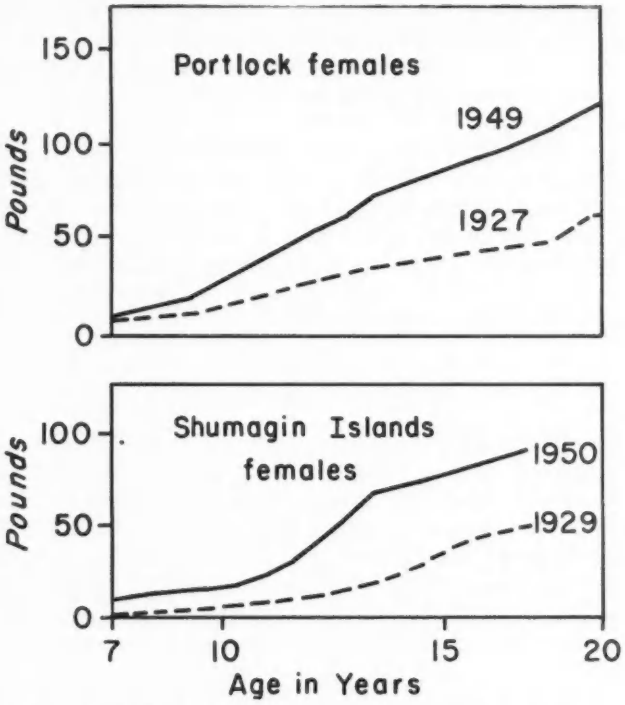

FIG. 1. Age-weight relationship of female halibut from Portlock and Shumagin Islands grounds, at two time periods corresponding to two population abundance levels as measured by the catch per skate.

TABLE I. Age-weight relationship of female halibut from Shumagin Islands and Portlock grounds. Weights shown are smoothed by 3's.

	Shumagin Islands		Portlock	
Age	1929	1950	1927	1949
	lbs	*lbs*	*lbs*	*lbs*
7	5.0	12.0	7.6	10.7
8	6.0	14.1	9.5	14.2
9	6.3	15.6	11.6	20.7
10	9.8	17.9	15.4	29.4
11	12.5	24.1	20.7	40.6
12	15.3	38.1	25.2	54.0
13	19.1	52.9	29.4	64.2
14	25.9	69.4	33.2	75.6
15	32.2	73.5	36.2	79.1
16	43.0	79.9	39.5	88.4
17	47.4	83.8	40.6	96.2
18	55.0	90.4	42.9	102.0
19	59.0	94.2	51.3	113.5
20	...	...	56.8	122.9

Sampling of the halibut populations in Area 3 by the chartered vessel tagging operations in which the sex ratio of the catch is known, and by the market sampling where the sex ratio is unknown, provided data which make possible the measurement of the change in the age-weight relationship of the halibut populations.

Due to the degree of intermingling of halibut from the Portlock-Albatross grounds with those of the Yakutat grounds and the Shumagin Islands grounds as shown by tagging, and inasmuch as halibut from the Portlock-Albatross grounds constitute over half of the Area 3[2] catch, this region was considered most representative of the Area 3 populations. Accordingly, the study of change in growth rates of the Pacific halibut and investigations of the causes underlying such a change was begun in this region.

METHOD OF MEASUREMENT

To facilitate the study and measurement of the otoliths, they were photographed on 35-mm film and positives were made (Southward, 1962). The positive image was projected at 20-times enlargement onto a table-top screen using an angled front-surfaced mirror. A scale was inserted in each frame, thereby permitting each image to be adjusted to a constant magnification and perpendicularity with the optical axis. The distance from the nucleus to the ventral edge, the radius, approximately at right angles to the anteroposterior axis, and the distance from the nucleus to the outer edge of each winter zone of each otolith was measured.

SOURCE OF MATERIALS

Otoliths with identifying sex data have been collected through the years from the halibut unsuitable for tagging on the Commission's tagging trips. Due to the possibility of a different otolith-radius body-length relationship for males and females, only those samples of otoliths where the sex of the individual fish was known were used in determining the relationship.

Since many of the tagging-trip otolith samples contained several thousand otoliths, the use of some method of sub-sampling these collections was necessary. Otoliths collected on tagging trips are arranged by capture date and sex, but no attempt is made to order them by length, weight or age. The sampling procedure adopted was to choose the first 10 otoliths of each age group of each sex for each tagging location. For the oldest and youngest ages of the age distribution where there were less than 10 individuals, all available otoliths were used. To encompass as great a distribution in space and time as possible, samples were chosen from the halibut populations between the Goose Islands grounds location and those in the Bering Sea and from trips taken between 1926 and 1957. When possible, samples were chosen so that each ground would have

[2]The grounds lying between Cape Spencer and the Shumagin Islands, Alaska. See the Pacific Halibut Fishery Regulations, International Pacific Halibut Commission, Seattle, Washington, for an exact description of Area 3.

observations at an early and late period in the history of exploitation. The sources of these material are given in Table II.

TABLE II. Source of data used in determining the relationship of otolith radius to body length.

Area	Year	Number by sex		
		Males	Females	Total
Goose Island	1926	44	36	80
Goose Island	1946–47	63	40	103
Goose Island	1955	93	149	242
Middle Hecate Strait	1953	61	42	103
Northern Hecate Strait	1953	69	56	125
Hecate Strait	1955	49	38	88
Timbered Islet	1926	41	35	76
Shelikof Bay	1958	31	37	68
Yakutat	1951	91	136	227
Portlock	1927	82	106	188
Portlock	1951	44	136	180
Karluk	1958	36	30	66
Portlock & vicinity	1957	93	72	165
Shumagin Islands	1929	72	88	160
Shumagin Islands	1950	88	108	196
Makushin Bay	1930	53	84	137
Makushin Bay	1956	19	62	81
Bering Sea	1957	133	86	219
TOTALS		1162	1341	2503

The age distribution, while not considered directly in the otolith-radius body-length relationship, ranges from fish of the year's brood to individuals 20 plus years old. The majority of halibut from age 4 to 6 years and older were obtained with conventional setline gear while the majority of fish less than 4 years of age were obtained with trawls (Kautz, MS, 1961). Several samples of commercial-sized trawl-caught halibut obtained from chartered vessel operations of the International Pacific Halibut Commission on the grounds in Queen Charlotte Sound and Hecate Strait were included. The age and length distributions of these samples overlap those of the sub-commercial sizes and the commercial sizes obtained with small mesh trawls and setline gear respectively.

FUNCTIONAL RELATIONSHIP BETWEEN OTOLITH-RADIUS AND BODY-LENGTH

The scatter of points in Fig. 2 of body length against otolith radius for males and females curves upward slightly. For illustrative purposes only, every tenth measurement is plotted. It is apparent from the increasing range of body-length with increasing otolith radius that the standard deviation of the mean body length is approximately proportional to the mean. So that the mean of the group of body lengths for each otolith radius would be independent of the standard

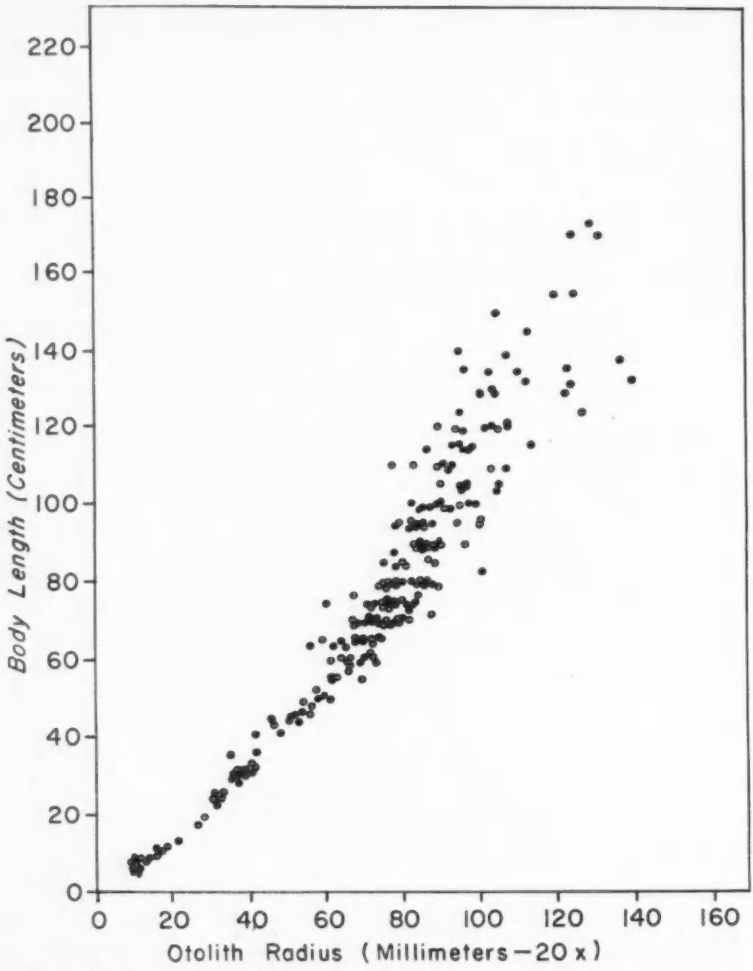

FIG. 2. Scatter diagram of body length plotted against otolith radius for data from Table II.

deviation of the mean, the data were transformed using natural logarithms. In addition, the transformation removed the curvilinearity of the data as shown by a scatter diagram of the transformed data (Fig. 3).

When the 2503 observations are plotted as a scatter diagram, identifying the sex, time and location of capture of each observation, no difference is apparent between the samples. However, the range of body-lengths for any particular otolith radius is large. Because of this large range, it is possible that the two sexes, the early and late time periods, or the southern and western fishing grounds,

might be better described by individual regression lines rather than a common line.

To test whether individual regression lines differ significantly, the data were examined by analysis of covariance. For each sex, tests were made of two hypotheses: (1) that the regression lines for each area and period of time differed significantly from each other in respect to slope and intercept ("test for a common line", Table III); and (2) that they differed in intercept but not in slope ("test for parallel lines"). The F-test rejects the first hypothesis conclusively for both sexes ($P<0.001$); the second hypothesis is rejected for females at the $P = 0.05$ level, while for males $P = 0.075$. This last might be an indication that the growth rate of male halibut has not changed as much as has the female halibut growth rate. However, it is probably a reflection of the shorter range of lengths avail-

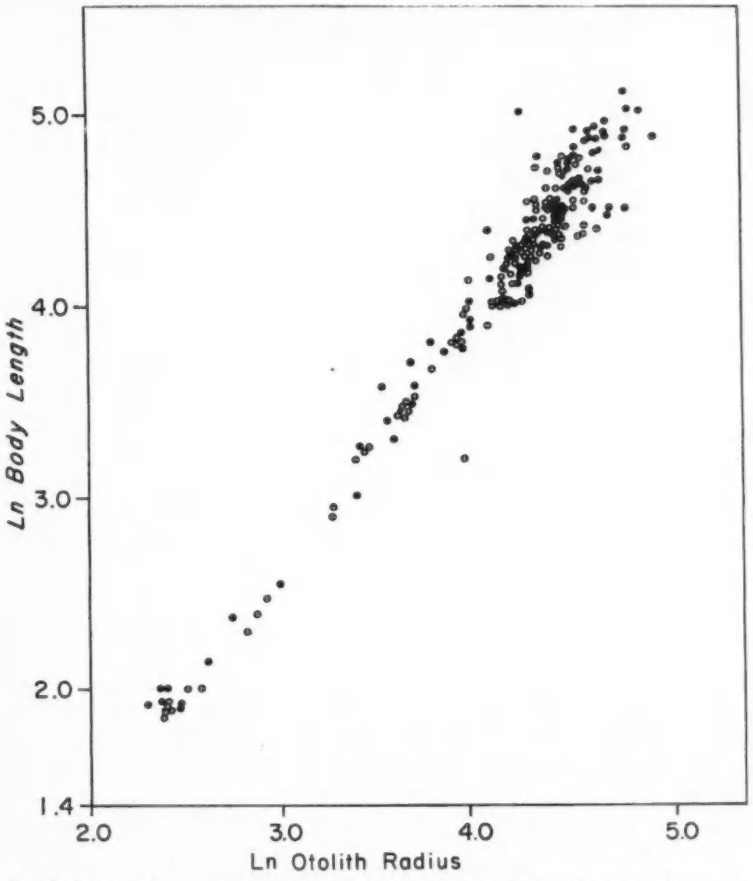

FIG. 3. Scatter diagram of the natural logarithm of body length against natural logarithm of otolith radius for data from Table II.

TABLE III. Comparison of southern early, southern recent, western early and western recent regressions of ln body-length on ln otolith-radius by analysis of covariance. Separate analysis for each sex.

Source	Sums of squares	Degrees of freedom	Mean square
Females			
HYPOTHESIS 1 — Test for a common line			
Deviations from a common line	23.15886		
Deviations from individual lines	22.58557	1333	0.01694
Deviations due to fitting a common line	0.57253	6	0.09542
F = 5.63282**			
HYPOTHESIS 2 — Test for parallel lines			
Deviations from parallel lines	22.91869		
Deviations from individual lines	22.58557	1333	0.01694
Deviations due to fitting parallel lines	0.33312	3	0.11104
F = 6.55490**			
Males			
HYPOTHESIS 1 — Test for a common line			
Deviations from a common line	16.78468		
Deviations from individual lines	16.57273	1154	0.01436
Deviations due to fitting a common line	0.21195	6	0.03532
F = 2.45961*			
HYPOTHESIS 2 — Test for parallel lines			
Deviations from parallel lines	16.67211		
Deviations from individual lines	16.57273	1154	0.01436
Deviations due to fitting parallel lines	0.09938	3	0.03313
F = 2.30710			

able for males, which results in less precise testing than in the case of the females where the range of lengths is considerably longer.

Inasmuch as the bulk of the data available for studying growth rates of the Pacific halibut are obtained from sampling the commercial catches, where it is impossible to identify the sex of the fish, a regression line based on a combination of male and female halibut data is indicated. To test the significance of differences between regression lines of body length on otolith radius for southern and western grounds during early (1925–1934) and recent (1935–1957) periods, with data for the sexes combined, analysis of covariance was again used (Table IV). The very significant F values ($P < 0.001$) for hypotheses (1) and (2) indicate again that these data are better described by the separate lines.

TABLE IV. Comparison of southern early, southern recent, western early and western recent regressions of ln body-length on ln otolith-radius by analysis of covariance. Data for both sexes combined.

HYPOTHESIS 1 — Test for a common line

Source	*Sums of squares*	*Degrees of freedom*	*Mean square*
Deviations from a common line	41.22547		
Deviations from individual lines	40.37185	2495	0.01618
Deviations due to fitting a common line	0.85362	6	0.14227
F = 8.79295**			

HYPOTHESIS 2 — Test for parallel lines

Source	*Sums of squares*	*Degrees of freedom*	*Mean square*
Deviations from parallel lines	40.86894		
Deviations from individual lines	40.37185	2495	0.01618
Deviations due to fitting parallel lines	0.49709	3	0.16569
F = 10.24042**			

TABLE V. Comparison of southern recent and western recent regressions of ln body-length on ln otolith-radius by analysis of covariance. Data for the sexes combined.

HYPOTHESIS 1 — Test for a common line

Source	*Sums of squares*	*Degrees of freedom*	*Mean square*
Deviations from a common line	31.56530		
Deviations from individual lines	31.23214	1858	0.01680
Deviations due to fitting a common line	0.33316	2	0.16658
F = 9.91547**			

HYPOTHESIS 2 — Test for parallel lines

Source	*Sums of squares*	*Degrees of freedom*	*Mean square*
Deviations from parallel lines	31.49822		
Deviations from individual lines	31.23214	1858	0.01680
Deviations due to fitting parallel lines	0.26608	1	0.26608
F = 15.83809**			

The results of the previous tests suggest that great variability is encountered in the relationship between otolith radius and body length. One source of the variability may be the inclusion of the material from the early period. The differences between the data from the southern and western grounds during the recent period (1935–1957), sexes combined, were examined by covariance analysis (Table V). This combination of data from the recent period represents current material. Again a rejection of the hypothesis (1) of a common slope and intercept and the rejection of the hypothesis (2) of parallel lines suggest that these data would be better described by individual regression lines.

The consistent rejection of the hypotheses of a common line and of parallel lines by the previous testing requires some discussion. When the regression lines for the southern and western grounds for early and recent periods, sexes combined, are plotted they appear to be similar (Fig. 4, Table VI). Although

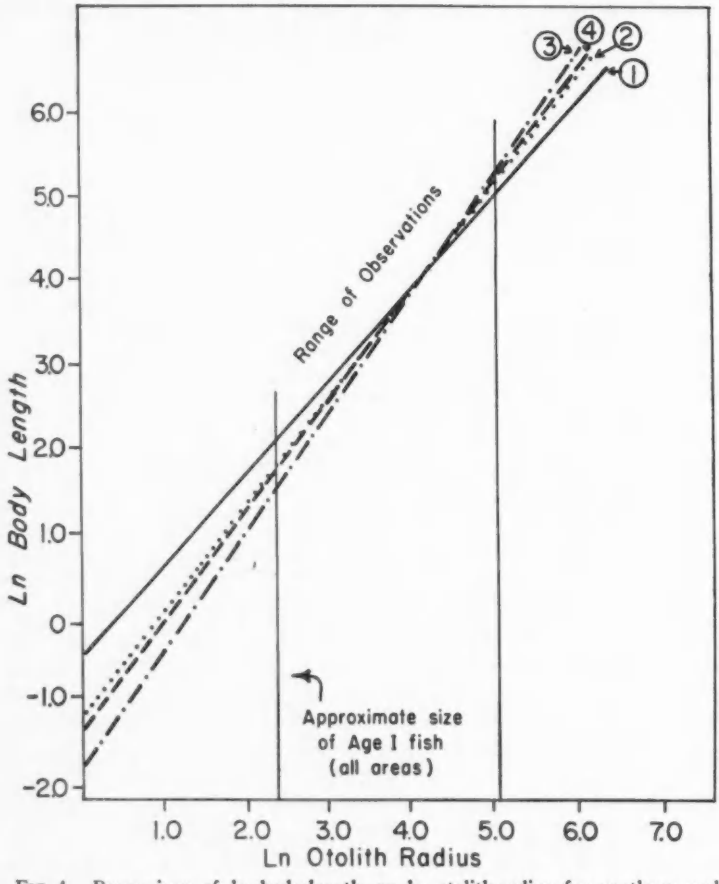

FIG. 4. Regressions of ln body-length on ln otolith-radius for southern and western grounds for early and recent capture periods, data for sexes combined.

mathematically these regressions are different, it is possible that the large range of body lengths and otolith radii and the large sample sizes have made the analysis of covariances too sensitive for the biological purposes intended. This implies that slight differences, much smaller than of practical importance, are being detected. Berkson (1938) discusses this point concerning testing with chi-square and Hodges and Lehmann (1954), discussing the testing of statistical hypotheses, point out that ". . . whenever the available data are extensive, the tests may become embarrassingly powerful . . .". It is the belief of the author that such a situation has occurred with this testing.

TABLE VI. Regression equations of body length on otolith radius for southern and western grounds for early and recent capture periods, sexes combined.

Southern grounds (1925–1934)	$Y = -0.43392 + 1.09345X$
Southern grounds (1935–1957)	$Y = -1.22287 + 1.28220X$
Western grounds (1925–1934)	$Y = -1.71960 + 1.40247X$
Western grounds (1935–1957)	$Y = -1.28838 + 1.32227X$

The standard error of estimate of the several regression lines (all data combined, western grounds (1925–1934), western grounds (1935–1957), southern grounds (1925–1934) and southern grounds (1935–1957)) indicates that the best estimate of body length is obtained from a regression based on the combination of all data (Table VII). While it is true that in some instances a slight decrease in the standard error of estimate could be obtained by using the individual regressions instead of the combined-data regression, in others the variance would be wider. In general the slight decrease in the standard error of estimate obtained by using individual regressions is not enough to warrant the increase in difficulty in application of the 4 regressions instead of the single regression based on a combination of all the data.

TABLE VII. Standard error of estimate and sample size for several regression lines of body length on otolith radius. Data for sexes combined.

Source	Standard error of estimate	Sample size
All data combined	0.1284	2503
Western grounds (1925–1935)	0.1222	485
Western grounds (1935–1957)	0.1219	1134
Southern grounds (1925–1935)	0.1120	156
Southern grounds (1935–1957)	0.1409	728

Accordingly, average body lengths are estimated, as a first approximation, by the regression of body lengths on otolith radii:

$$\ln Y = -1.32086 + 1.30795(\ln X) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where Y = body length and X = otolith radius.

CONFIDENCE LIMITS OF THE ESTIMATED BODY LENGTHS

The 95% confidence interval about this line for average estimates based on the sample of approximately 2500 measurements extends from 64.4 to 65.1 cm, a range of 0.7 cm, at a projected otolith radius of 66 mm. The 95% confidence interval about this line for individual estimates based on the same sample extends from 50.3 to 83.3 cm, a range of 33 cm, at a projected otolith radius of 66 mm. The large confidence interval for individual estimates reflects the great variability in fish length at a given otolith size, as indicated by the analysis of covariance tests.

In practice individual estimates are not made, but rather average estimates based on the regression of 2503 otolith measurements are made for samples of approximately 10 to 20 individuals in any age group. The confidence interval[3] for these estimates is given by:

$$\overline{\ln(Y)} \pm 1.96 S_{y.x,2503} \left(\frac{1}{n} + \frac{1}{N} + \frac{\left(\overline{\ln(X_n)} - \overline{\ln(X_N)}\right)^2}{\sum_{i=1}^{2503} \left(\ln(X_i) - \overline{\ln(X_N)}\right)^2} \right)^{\frac{1}{2}} \quad \ldots\ldots\ldots (2)$$

where: $\overline{\ln(Y)}$ is the mean body length of the sample determined from the regression equation, $S_{y.x,2503}$ is the pooled variance (0.1284) of the data used in determining the relationship of body length to otolith radius, N is the number of observations in the relationship (2503), n is the number of observations in each sample, $\overline{\ln(X_N)}$ is the mean of the otolith radii used in the relationship, $\ln(X_i)$ is the individual observation used in the relationship and $\overline{\ln(X_n)}$ is the mean of the otolith radii of each sample.

As an example, the 95% confidence interval is calculated from (2) for the sample of 14 halibut shown in Table VIII:

$$\overline{\ln(Y)} = 4.60417$$

$$S_{y.x,2503} = 0.1284$$

$$\frac{1}{n} = \frac{1}{14} = 0.071429$$

$$\frac{1}{N} = \frac{1}{2503} = 0.00399$$

$$\overline{\ln(X_n)} = 4.52404$$

$$\overline{\ln(X_N)} = 4.19831$$

$$\sum_{i=1}^{2503} \left(\ln(X_i) - \overline{\ln(X_N)}\right)^2 = 722.12724$$

95% limits of logarithms = 4.535, 4.673

95% limits of size = 93 cm, 107 cm

[3]The author is indebted to Mr Charles O. Junge, Fisheries Research Institute, University of Washington, for help in determining this confidence interval.

The limits for the logarithms, above, are obtained directly from (2); their antilogarithms are the actual lengths shown in the last line. The range for 95% confidence is 14 cm of body length at a projected otolith radius of 93 mm and average computed body length of 100 cm.

TABLE VIII. Sample of fourteen 10-year-old halibut (sample No. R387) used to compute the confidence interval described in the text. Body lengths were calculated from equation (1) of the text.

Projected otolith radius (X_n)	Calculated body length (Y)
mm	*cm*
95	104
108	122
86	90
77	78
87	92
87	92
103	114
98	108
83	86
90	96
107	120
100	110
86	90
90	96
G.M. 92.2	99.9

VERIFICATION OF OTOLITH-SIZE BODY-LENGTH RELATIONSHIP

The otoliths from recovered tagged halibut provide material which can be used in checking the validity of the calculated body lengths. If the otolith-radius body-length relationship is valid, the lower confidence limit of the calculated average length of the halibut at the beginning of the year of tagging and the upper confidence limit of the calculated length of the halibut at the end of the growth zone of the year of tagging should be below and above, respectively, the average measured length of the fish at the time of tagging.

To test the above assumption, otoliths from halibut recovered in 1954 and 1955 from the Goose Islands tagging experiments were measured, and the otolith radius was converted to body length using the common regression lines of otolith radius on body length. A summary of these data is given in Table IX.

The 1954 material covers ages 8 to 16. Between age-groups 10 to 16, excluding age 15, the measured average body length of halibut within each age group at the time of tagging falls between the calculated average body lengths based on the otolith regression at the beginning and ending of the tagging year.

TABLE IX. Lengths computed from otoliths of halibut tagged in 1951 on the Goose Island grounds and recovered by the commercial fishery in 1954 and 1955. The average length as measured at time of tagging is shown in column 2. Column 4 is the computed length at the last annulus formed before tagging, and column 3 shows the lower 95% confidence limit for this length. Column 5 is the computed length at the first annulus after tagging, and column 6 is the upper 95% confidence limit for same. The actual lengths (column 2) usually lie between those computed from the two annuli (columns 4 and 5), and in almost all cases they lie between the two limits shown (columns 3 and 6).

1	2	3	4	5	6	7
		Computed lengths				
Age	Average body length at tagging	Lower limit	Before tagging	After tagging	Upper limit	No. in sample
		1954 *recoveries*				
8	80	50	58	66	76	3
9	83	53	63	72	86	2
10	73	61	68	74	82	6
11	74	66	72	79	86	8
12	77	66	72	77	84	9
13	85	76	82	87	94	10
14	94	80	89	96	106	6
15	91	79	86	90	97	10
16	106	93	103	106	117	6
		1955 *recoveries*				
8	69	46	59	68	87	1
9	81	54	70	78	100	1
10	75	52	58	70	78	6
11	79	63	71	74	88	4
12	81	68	74	81	88	10
13	85	72	80	89	97	8
14	80	69	77	82	91	7
15	92	81	91	98	110	5
17	94	72	93	96	123	1
18	91	62	80	85	109	1
22	105	79	102	105	131	1

At age 15, the average tagging length is only 1 cm longer than the calculated length and is well below the upper confidence limit. The average tagging length of the age 9 fish is beyond the calculated length but inside the confidence limit. The average tagging length of the age 8 fish is outside the calculated length as well as the upper confidence limit. This is probably due to the seemingly large measurement for 1 fish of the 3 in this age group.

The 1955 material covers ages 8 to 22. The average measured length at the time of tagging of the age group for ages 12, 13, 14, 15, 17 and 22 fell within the range of the calculated average length at the beginning of the year prior to tagging and at the ending of the year of tagging for each age group. The average measured lengths at the time of tagging for ages 8 to 11 and 18 were slightly

greater than the largest calculated average length but well inside the upper and lower confidence limits.

In general the data support the assumption that if the otolith-radius body-length relationship is valid the average measured length at the time of tagging will be between the calculated length at the beginning and ending of the year of tagging. In practically all of the age groups, with a few exceptions, the tagging length is near that calculated for the end of the year of tagging. This is understandable since tagging was done in October. By this time the fish had obtained practically all of their annual growth. Several other factors might influence the position of the calculated lengths in relation to the tagging lengths. Since the fishery takes the larger of the younger age groups and the otolith-radius body-length relationship is based on an average, an underestimation of body length might result when otoliths of the younger ages from the commercial catch are used. The numbers of fish in the younger age groups are small and the underestimation of body-length might be chance variation. A differential rate of growth between sexes, which in these calculations has been assumed to be of secondary importance, could cause this underestimation.

Comparison of the average measured body-length of an age group with the average calculated body-length and the 95% confidence interval at the beginning and ending of the year of tagging indicates that the otolith-radius body-length relationship is valid and that an average body length can be calculated at earlier ages within each age group. This will permit the reconstruction of the growth pattern of successive year classes and determination of the growth rate of each year class at various stock levels as indicated by the catch per skate.

CALCULATED BODY LENGTHS OF HALIBUT FROM PORTLOCK-ALBATROSS GROUNDS 1935–1957

Otoliths from the Commission's tagging operation on Portlock bank in 1926 and from market samples collected from the commercial landings from Portlock-Albatross grounds between 1935 and 1957 were measured and the otolith measurements converted to average body lengths for each age of the year-classes involved. The market samples consisted of one sample of approximately 140 otoliths each year from 1935 to 1945 and from 1949 to 1957. There was no sampling of the landings between 1946 and 1949. In each case the samples used were those taken during May and June. The back-calculation method of determining lengths of halibut at earlier ages of each year class permits the 4-year gap in the 1940's (when sampling was not done) to be filled in, as well as extending the samples to 1920. A summary of these data is given in Table X.

The percentage deviation in length from an approximately 37-year average[4] for each age from 1 to 20 between 1920 and 1957 is given in Table XI. To illustrate the change in average length that has occurred since 1920, every third age starting with age 1 is shown in Fig. 5.

[4]Due to the distribution of ages the 37-year average decreases by one year starting with age 7 until it is a 31-year average at age one.

TABLE X. Source of market samples used in computing the percentage deviation of body lengths from 1920 to 1957. All trips are from Portlock-Albatross grounds.

Year	Date	Sample No.	Boat	Number fish in sample
1935	May 2	91	*Helgoland*	172
1936	May 29	202	*Vansee*	131
1937	June 9	311	*North*	126
1938	July 14	408	*Chelan*	128
1939	April 24	450	*Eagle*	119
1940	June 24	563	*Brisk*	127
1941	April 23	607	*McKinley*	124
1942	June 5	688	*Ilene*	125
1943		No sample		
1944	July 3	741	*Venture*	122
1949	May 19	828	*McKinley*	163
1950		No sample		
1951	July 5	897	*Anne*	125
1952	May 29	922	*Trinity*	118
1953	July 7	987	*Soupfin*	118
1954	June 18	1035	*Flying Tiger*	116
1955	June 23	1098	*McKinley*	130
1956	June 6	1137	*Zenith*	134
1957	June 21	1220	*St. John*	126

The comparison of apparently fast- or slow-growing year-classes, which may be traced in Fig. 5, should be avoided or done cautiously since measurements made from otoliths of fish which belong to the older age-groups are present in varying degrees in the younger age-groups. For example, 16-year-old fish contributed some data to the averages for each age less than 16. The examination of the growth rate of individual year-classes and the question of density-dependent growth, which has been examined and is complicated, will be discussed in a later paper.

The percentage deviations of average length of the young halibut from ages 1 to 4 show little or no trend and the fluctuations about the average line seem to be random or at least non-directional with time. A trend of increasing deviations of average body-length with time is evident at approximately age 5 and continues through the older ages. By age 7 it is definite and by age 10 and older is very pronounced.

DISCUSSION

The change in growth rate that is indicated in Fig. 1 is great. The two periods compared in the figure represent different population density levels as measured by catch per skate. The older fish in the catches in 1927 and 1929, from Portlock-Albatross and Shumagin Islands grounds respectively, originated and grew under conditions of relatively unfished population densities (IPHC, 1954). The older fish in the catches of 1949 and 1950, taken from the same

TABLE XI. Deviations (in percentage) of average calculated body lengths from an approximately 37-year average, for each year between 1920 and 1957. The calculated length for each year at each age is the average of lengths computed from all older fish. See the text, p. 353, for details.

Year	Age 1 Av. length 6.9 cm		Age 2 Av. length 17.5 cm		Age 3 Av. length 29.4 cm		Age 4 Av. length 40.7 cm	
	Length	Deviation	Length	Deviation	Length	Deviation	Length	Deviation
	cm	*%*	*cm*	*%*	*cm*	*%*	*cm*	*%*
1920	6.1	−11.6	15.7	−10.3	27.4	− 6.8	36.5	−10.3
1921	6.1	−11.6	14.3	−18.3	28.4	− 3.4	37.6	− 7.6
1922	6.1	−11.6	15.7	−10.3	25.9	−11.9	39.3	− 3.4
1923	6.1	−11.6	16.2	− 7.4	27.9	− 5.1	38.4	− 5.6
1924	6.9	0	17.0	− 2.9	27.9	− 5.1	38.4	− 5.6
1925	6.5	− 5.8	16.6	− 5.1	31.1	+ 5.8	37.3	− 3.4
1926	6.9	0	16.2	− 7.4	30.0	+ 2.0	42.2	+ 3.7
1927	7.6	+10.1	19.0	+ 8.6	31.0	+ 5.4	39.9	− 2.0
1928	6.9	0	19.4	+10.9	37.8	+28.6	41.0	+ 0.7
1929	6.9	0	17.0	− 2.9	32.4	+10.2	41.0	+ 0.7
1930	6.9	0	17.5	0	30.0	+ 2.0	42.2	+ 3.7
1931	6.5	− 5.8	16.6	− 5.1	31.1	+ 5.8	41.0	+ 0.7
1932	6.9	0	17.0	− 2.9	29.0	− 1.4	42.7	+ 4.9
1933	6.5	− 5.8	18.5	+ 5.7	30.0	+ 2.0	41.0	+ 0.7
1934	6.9	0	17.0	− 2.9	29.5	+ 0.3	41.6	+ 2.2
1935	6.9	0	17.0	− 2.9	29.0	− 1.4	41.6	+ 2.2
1936	7.6	+10.1	18.0	+ 2.9	31.1	+ 5.8	41.0	+ 0.7
1937	8.0	+15.9	19.4	+10.9	31.1	+ 5.8	42.2	+ 3.7
1938	7.6	+10.1	19.0	+ 8.6	31.1	+ 5.8	41.6	+ 2.2
1939	7.6	+10.1	18.5	+ 5.7	30.5	+ 3.7	41.0	+ 0.7
1940	7.6	+10.1	17.0	− 2.9	31.7	+ 7.8	41.0	+ 0.7
1941	6.9	0	19.0	+ 8.6	30.0	+ 2.0	42.2	+ 3.7
1942	7.6	+10.1	19.0	+ 8.6	33.3	+13.3	41.0	+ 0.7
1943	7.6	+10.1	18.0	+ 2.9	33.3	+13.3	44.5	+ 9.3
1944	6.9	0	18.0	+ 2.9	31.1	+ 5.8	42.2	+ 3.7
1945	6.9	0	18.0	+ 2.9	31.1	+ 5.8	42.2	+ 3.7
1946	6.9	0	18.0	+ 2.9	30.0	+ 2.0	42.2	+ 3.7
1947	6.1	−11.6	18.0	+ 2.9	29.0	− 1.4	38.8	− 4.7
1948	6.9	0	17.0	− 2.9	29.0	− 1.4	38.8	− 4.7
1949	6.9	0	17.0	− 2.9	29.0	− 1.4	38.8	− 4.7
1950	6.9	0	19.0	+ 8.6	29.0	− 1.4	38.8	− 4.7
1951	...	...	17.0	− 2.9	32.4	+10.2	21.0	+ 0.7
1952	...	...	...	...	30.0	+ 2.0	45.6	+12.0
1953	...	...	...	...	...	...	38.8	−11.7

TABLE XI — continued

Year	Age 5 Av. length 49.4 cm		Age 6 Av. length 57.2 cm		Age 7 Av. length 64.7 cm		Age 8 Av. length 71.3 cm	
	Length	Deviation	Length	Deviation	Length	Deviation	Length	Deviation
	cm	%	*cm*	%	*cm*	%	*cm*	%
1920	45.6	− 7.7	51.6	− 9.8	60.3	− 6.8	64.7	− 9.3
1921	44.5	− 9.9	51.6	− 9.8	57.0	−11.9	65.3	− 8.4
1922	45.0	− 8.9	49.8	−12.9	57.6	−11.0	62.8	−11.9
1923	47.4	− 4.0	51.6	− 9.8	56.5	−12.7	62.8	−11.9
1924	45.6	− 7.7	54.1	− 5.4	57.6	−11.0	61.4	−13.9
1925	46.8	− 5.3	54.1	− 5.4	60.3	− 6.8	62.8	−11.9
1926	47.4	− 4.0	54.1	− 5.4	60.3	− 6.8	65.3	− 8.4
1927	50.4	+ 2.0	55.3	− 3.3	60.3	− 6.8	66.6	− 6.6
1928	48.0	− 2.8	56.5	− 1.2	59.6	− 7.9	63.4	−11.1
1929	48.0	− 2.8	55.3	− 3.3	62.8	− 2.9	65.9	− 7.6
1930	50.4	+ 2.0	55.3	− 3.3	62.1	− 4.0	68.4	− 4.1
1931	50.4	+ 2.0	57.6	+ 0.7	62.1	− 4.0	67.2	− 5.8
1932	50.4	+ 2.0	57.0	− 0.3	64.7	0	67.8	− 4.9
1933	51.6	+ 4.4	58.3	+ 1.9	64.1	− 0.9	71.7	+ 0.6
1934	49.3	− 0.2	56.5	− 1.2	65.3	+ 0.9	71.7	+ 0.6
1935	49.3	− 0.2	56.5	− 1.2	65.3	+ 0.9	71.7	+ 0.6
1936	49.3	− 0.2	55.3	− 3.3	62.8	− 2.9	71.7	+ 0.6
1937	51.0	+ 3.2	56.5	− 1.2	62.8	− 2.9	69.1	− 2.1
1938	51.6	+ 4.4	59.0	+ 3.1	64.1	− 0.9	69.1	− 3.1
1939	50.4	+ 2.0	61.4	+ 7.3	67.8	+ 4.8	71.7	+ 0.6
1940	49.3	− 0.2	57.6	+ 0.7	70.4	+ 8.8	74.3	+ 4.2
1941	48.0	− 2.8	57.6	+ 0.7	66.6	+ 2.9	77.0	+ 8.0
1942	51.6	+ 4.4	57.6	+ 0.7	65.3	+ 0.9	73.0	+ 2.4
1943	51.6	+ 4.4	61.4	+ 7.3	66.6	+ 2.9	73.0	+ 2.4
1944	54.1	+ 9.5	59.0	+ 3.1	69.1	+ 6.8	74.3	+ 4.2
1945	50.4	+ 2.0	62.8	+ 9.8	67.8	+ 4.8	74.3	+ 4.2
1946	51.6	+ 4.4	60.3	+ 5.4	71.7	+10.8	75.7	+ 6.2
1947	50.4	+ 2.0	60.3	+ 5.4	67.8	+ 4.8	79.6	+11.6
1948	48.0	− 2.8	59.0	+ 3.1	67.8	+ 4.8	75.7	+ 6.2
1949	48.0	− 2.8	56.5	− 1.2	67.8	+ 4.8	75.7	+ 6.2
1950	49.3	− 0.2	57.6	+ 0.7	64.1	− 0.9	74.3	+ 4.2
1951	49.3	− 0.2	59.0	+ 3.1	66.6	+ 2.9	71.7	+ 0.6
1952	50.4	+ 2.0	60.3	+ 5.4	69.1	+ 6.8	75.7	+ 6.2
1953	56.5	+14.4	59.0	+ 3.1	69.1	+ 6.8	78.3	+ 9.8
1954	48.0	− 2.8	67.8	+18.5	69.1	+ 6.8	78.3	+ 9.8
1955	...	...	56.5	− 1.2	77.0	+19.0	79.6	+11.6
1956	...	...	...	...	64.1	− 0.9	87.7	+23.0
1957	...	...	...	...	...	...	71.7	+ 0.6

TABLE XI — continued

Year	Age 9 Av. length 77.3 cm		Age 10 Av. length 82.7 cm		Age 11 Av. length 87.9 cm		Age 12 Av. length 94.0 cm	
	Length	Deviation	Length	Deviation	Length	Deviation	Length	Deviation
	cm	%	*cm*	%	*cm*	%	*cm*	%
1920	65.9	-14.7	70.4	-14.9	73.6	-16.3	75.0	-20.2
1921	70.4	- 8.9	71.0	-14.1	74.3	-15.5	77.2	-17.9
1922	70.4	- 8.9	73.0	-11.7	76.3	-13.2	79.6	-15.3
1923	69.1	-10.6	76.3	- 7.7	81.0	- 7.8	81.6	-13.2
1924	67.8	-12.3	75.0	- 9.3	82.3	- 6.4	84.3	-10.3
1925	65.3	-15.5	74.3	-10.2	81.6	- 7.2	87.7	- 6.7
1926	68.4	-11.5	70.4	-14.9	73.9	-15.9	87.7	- 6.7
1927	71.7	- 7.2	75.0	- 9.3	75.7	-13.9	85.0	- 9.6
1928	67.8	-12.3	71.7	-13.3	...	...	...	...
1929	69.1	-10.6	71.7	-13.3	76.3	-13.2	...	...
1930	71.0	- 8.2	74.0	-10.5	75.7	-13.9	81.6	-13.2
1931	75.0	- 3.0	77.0	- 6.9	80.3	- 8.6	80.3	-14.6
1932	75.0	- 3.0	82.3	- 0.5	82.9	- 5.7	85.7	- 8.8
1933	74.3	- 3.9	81.6	- 1.3	88.4	+ 0.6	89.1	- 5.2
1934	77.0	- 0.4	83.6	+ 1.1	86.4	- 1.7	93.9	- 0.1
1935	77.0	- 0.4	83.6	+ 1.1	86.4	- 1.7	93.3	- 0.7
1936	78.3	+ 1.3	82.3	- 0.5	89.1	+ 1.4	87.7	- 6.7
1937	78.3	+ 1.3	83.6	+ 1.1	89.1	+ 1.4	94.6	+ 0.6
1938	79.6	+ 3.0	85.0	+ 2.8	87.7	- 0.2	94.6	+ 0.6
1939	77.0	- 0.4	82.3	- 0.5	90.5	+ 3.0	93.3	- 0.7
1940	77.0	- 0.4	82.3	- 0.5	87.7	- 0.2	96.1	+ 2.2
1941	79.6	+ 3.0	83.6	+ 1.1	86.4	- 1.7	94.6	+ 0.6
1942	82.3	+ 6.5	86.4	+ 4.5	90.5	+ 3.0	90.5	- 3.7
1943	78.3	+ 1.3	91.9	+11.1	89.1	+ 1.4	102.0	+ 8.5
1944	79.6	+ 3.0	85.0	+ 2.8	97.5	+10.9	94.6	+ 0.6
1945	79.6	+ 3.0	85.0	+ 2.8	90.5	+ 3.0	105.0	+11.7
1946	85.0	+10.0	87.7	+ 6.0	91.9	+ 4.6	98.8	+ 5.1
1947	82.3	+ 6.5	91.9	+11.1	94.6	+ 7.6	97.5	+ 3.7
1948	86.4	+11.8	90.5	+ 9.4	98.8	+12.4	102.0	+ 8.5
1949	82.3	+ 6.5	93.3	+12.8	97.5	+10.9	106.0	+12.8
1950	82.3	+ 6.5	87.7	+ 6.0	98.8	+12.4	98.8	+ 5.1
1951	82.3	+ 6.5	89.1	+ 7.7	94.6	+ 7.6	106.0	+12.8
1952	75.7	- 2.1	90.5	+ 9.4	96.1	+ 9.3	98.8	+ 5.1
1953	85.0	+10.0	86.4	+ 4.5	97.5	+10.9	104.0	+10.6
1954	86.4	+11.8	91.9	+11.1	94.6	+ 7.6	108.0	+14.9
1955	87.7	+13.4	91.9	+11.1	104.0	+18.3	109.0	+16.0
1956	87.7	+13.4	94.6	+14.4	98.8	+12.4	105.0	+11.7
1957	89.1	+15.3	90.5	+ 9.4	93.3	+ 6.1	114.0	+21.3

TABLE XI — continued

Year	Age 13 Av. length 98.9 cm		Age 14 Av. length 101.9 cm		Age 15 Av. length 106.4 cm		Age 16 Av. length 109.3 cm	
	Length	Deviation	Length	Deviation	Length	Deviation	Length	Deviation
	cm	%	*cm*	%	*cm*	%	*cm*	%
1920	...	...	75.7	−25.7	...	...	...	...
1921	78.3	−20.3	...	...	79.6	−25.2	...	...
1922	81.0	−18.1	82.3	−19.2	...	...	82.3	−24.7
1923	84.3	−14.8	84.3	−17.3	86.4	−18.8	...	...
1924	87.7	−11.3	89.1	−12.6	87.7	−17.6	89.1	−18.5
1925	89.1	− 9.9	91.9	− 9.8	93.3	−12.3	91.9	−15.9
1926	93.3	− 5.7	93.3	− 8.4	97.5	− 8.4	98.8	− 9.6
1927	93.9	− 5.1	97.5	− 4.3	98.8	− 7.1	102.0	− 6.7
1928	80.3	−18.8	...	...	...	...	...	...
1929	...	...	86.4	−15.2	...	...	...	...
1930	...	...	...	...	91.9	−13.6	...	...
1931	86.4	−12.6	...	...	...	...	96.1	−12.1
1932	85.0	−14.1	90.5	−11.2	...	...	...	...
1933	90.5	− 8.5	89.8	−11.9	96.1	− 9.7	...	...
1934	100.0	+ 1.1	99.4	− 2.5	102.0	− 4.1	98.8	− 9.6
1935	100.0	+ 1.1	98.8	− 3.0	102.0	− 4.1	98.8	− 9.6
1936	98.8	− 0.1	105.0	+ 3.0	105.0	− 1.3	109.0	− 0.3
1937	97.5	− 1.4	108.0	+ 6.0	114.0	+ 7.1	109.0	− 0.3
1938	100.0	+ 1.1	100.0	− 1.9	108.0	+ 1.5	123.0	+12.5
1939	98.8	− 0.1	108.0	+ 6.0	104.0	− 2.2	109.0	− 0.3
1940	97.5	− 1.4	100.0	− 1.9	110.0	+ 3.4	104.0	− 4.8
1941	105.0	+ 6.2	105.0	+ 3.0	104.0	− 2.3	114.0	+ 4.3
1942	100.0	+ 1.1	105.0	+ 3.0	100.0	− 6.0	96.1	−12.1
1943	98.8	− 0.1	116.0	+13.8	120.0	+12.8	108.0	− 1.2
1944	109.0	+10.2	105.0	+ 3.0	123.0	+15.6	125.0	+14.4
1945	96.1	− 2.8	127.0	+24.6	85.0	−20.1	...	...
1946	111.0	+12.2	100.0	− 1.9	133.0	+25.0	90.5	−17.2
1947	105.0	+ 6.2	118.0	+15.8	106.0	− 0.4	138.0	+26.3
1948	105.0	+ 6.2	110.0	+ 7.9	122.0	+14.7	111.0	+ 1.6
1949	109.0	+10.2	110.0	+ 7.9	118.0	+10.9	127.0	+16.2
1950	106.0	+ 7.2	109.0	+ 7.0	106.0	− 0.4	123.0	+12.5
1951	109.0	+10.2	103.0	+ 6.0	113.0	+ 6.2	110.0	+ 0.6
1952	113.0	+14.3	105.0	+ 3.0	110.0	+ 3.4	116.0	+ 6.1
1953	106.0	+ 7.2	109.0	+ 7.0	109.0	+ 2.4	114.0	+ 4.3
1954	110.0	+11.2	111.0	+ 8.9	110.0	+ 3.4	116.0	+ 6.1
1955	113.0	+14.3	110.0	+ 7.9	113.0	+ 6.2	120.0	+ 9.8
1956	108.0	+ 9.2	119.0	+16.8	125.0	+17.5	122.0	+11.6
1957	114.0	+15.3	110.0	+ 7.9	131.0	+23.1	127.0	+16.2

TABLE XI — continued

Year	Age 17 Av. length 112.7 cm		Age 18 Av. length 118.5 cm		Age 19 Av. length 120.4 cm		Age 20 Av. length 119.0 cm	
	Length	Deviation	Length	Deviation	Length	Deviation	Length	Deviation
	cm	%	*cm*	%	*cm*	%	*cm*	%
1920	...	...	...	...	...	...	...	...
1921	...	...	...	...	...	...	...	...
1922	...	...	...	...	...	...	...	...
1923	85.0	-24.6	...	...	...	...	...	...
1924	...	...	93.3	-21.3	...	...	...	...
1925	93.3	-12.2	...	...	90.5	-24.2	...	...
1926	94.6	-16.1	97.5	-17.7	...	...	93.3	-21.6
1927	105.0	- 6.8	98.8	-16.6	101.0	-16.1	...	...
1928	...	...	...	...	...	...	...	...
1929	...	...	...	...	...	...	...	...
1930	...	...	...	...	...	...	...	...
1931	...	...	...	...	...	...	...	...
1932	104.0	- 7.7	...	...	...	...	...	...
1933	...	...	108.0	- 8.9	...	...	...	...
1934	104.5	- 7.3	...	...	...	...	114.0	- 4.2
1935	105.0	- 6.8	...	...	...	...	114.0	- 4.2
1936	93.3	-17.2	110.0	- 7.2	...	...	105.0	-11.8
1937	127.0	+12.7	...	...	...	...	...	...
1938	120.0	+ 6.5	...	...	...	...	...	...
1939	129.0	+14.5	123.0	+ 3.8	...	...	...	...
1940	...	...	...	...	129.0	+ 7.1	...	...
1941	108.0	- 4.2	...	...	...	...	135.0	+13.4
1942	111.0	- 1.5	143.0	+20.7	...	...	...	...
1943	...	...	...	...	...	...	...	...
1944	114.0	+ 1.2	...	...	149.0	+23.8	...	...
1945	...	...	...	...	...	...	...	...
1946	...	...	...	...	...	...	...	...
1947	93.3	-17.2	...	...	...	...	...	...
1948	146.0	+29.5	98.8	-16.6	...	...	...	...
1949	118.0	+ 4.7	150.0	+26.6	104.0	-13.6	...	...
1950	120.0	+ 6.5	...	...	...	...	...	...
1951	128.0	+13.6	127.0	+ 7.2	...	...	...	...
1952	110.0	- 2.4	...	...	113.0	- 6.1	...	...
1953	123.0	+ 9.1	110.0	- 7.2	...	...	...	...
1954	119.0	+ 5.6	131.0	+10.5	118.0	- 2.0	...	...
1955	113.0	+ 0.3	127.0	+ 7.2	140.0	+16.3	125.0	+ 5.0
1956	118.0	+ 4.7	125.0	+ 5.5	131.0	+ 8.8	135.0	+13.4
1957	136.0	+20.7	135.0	+13.9	128.0	+ 6.3	131.0	+10.1

grounds, originated and grew under conditions of a fished population. Twenty-year old female halibut from Portlock-Albatross grounds in 1949 weighed approximately 122 lb (55 kg) dressed head-on gills-out, compared to 56 lb (25 kg) for a fish of the same age and sex in 1927. There is also an inverse relationship suggested between numbers of halibut and their weight in some of the stock-composition data. However, the density-dependent growth rate which is implied is not easily demonstrated.

Figure 5 again demonstrates the change in length by age for halibut on the Portlock grounds. The trend of increasing length with time, which begins in the early and middle 1930's, seems to be associated with the year-classes that originated near the time of low population density. The lack of trend, in all years, of ages up to approximately age 4 — that is fish which are not freely

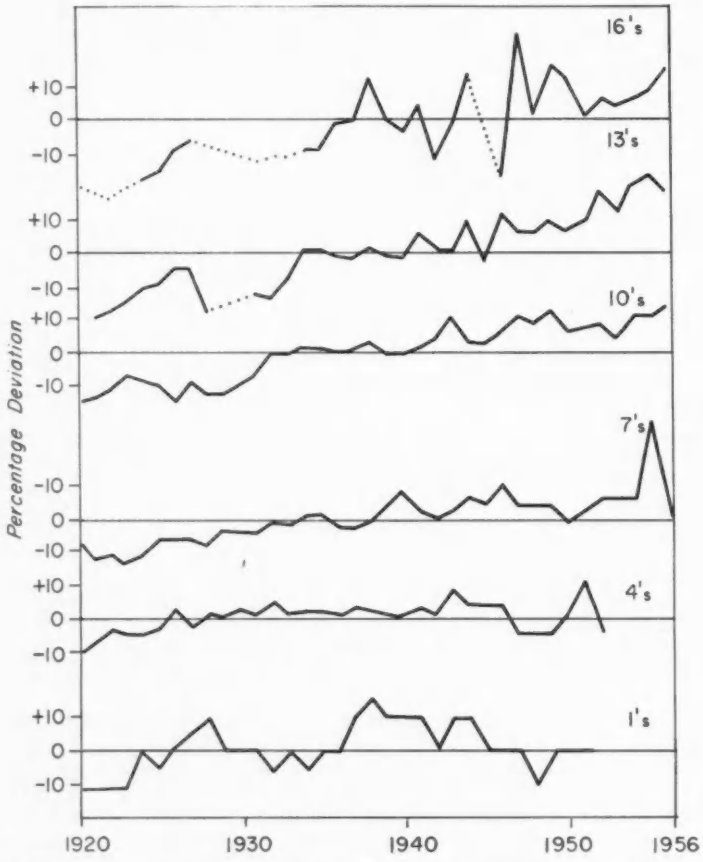

FIG. 5. Percentage deviation of computed body length from the grand mean for each age for Portlock-Albatross data (1920–1957).

intermingled with the mature commercial stock — suggests that the density of the adult component of the population does not influence the growth of the younger ages perceptibly.

The possibility of a change in environmental conditions resulting in a change in average weight for each age must not be overlooked. Unfortunately, adequate oceanographic data are lacking for most of the time and the region covered by this study. Ketchen (1956) has discussed possible effects of oceanographic changes related to air temperature changes on growth of halibut in the eastern Pacific, while Bell and Pruter (1958) have pointed out some of the pitfalls encountered in attempting to relate biological phenomenon such as growth with inadequate hydrographical and meteorological data.

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NOTES

First Record of the Great White Shark (*Carcharodon carcharias*) from British Columbia

A shark measuring 11 feet and 3 inches (3.4 m) was found stranded on the beach at Creek Mouth, Island Bay, on the east coast of the Queen Charlotte Islands (Latitude 52°21′06″N, Longitude 131°24′W) on October 24, 1961, by Mr K. R. Harley, an officer of the Canada Department of Fisheries. Mr Harley identified the species as the great white or man-eater shark, *Carcharodon carcharias* (Linnaeus), according to the body form and teeth. His description was accompanied by a tooth specimen which confirms the identification. The tooth, characteristic of the genus, is triangular, with slightly concave margins, coarsely serrated edges, and lacking lateral denticles.

This specimen is a northern record for the species in the north Pacific and a first occurrence for British Columbia. Previous northern records for the northeastern Pacific Ocean are from Washington (K. Bonham, 1942, *Copeia*, No. 4, pp. 264–266). Weights of two Washington specimens measuring about 12 feet were between 800 and 1000 pounds. Weight of the British Columbia specimen was estimated to be 1000 lb (450 kg).

This shark has been characterized as "the most voracious of fish-like vertebrates". Large prey, including sea lions, seals, sturgeons and sea turtles, are devoured practically intact. It is perhaps the only shark which can be authentically charged with unprovoked attacks on small boats or swimmers.

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